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CAMERA TRAPPING FOR THE STUDY AND CONSERVATION OF TROPICAL CARNIVORES

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ABSTRACT. — Past studies on tropical carnivores and other secretive animals relied on indirect evidence of animal presence such as tracks, scats, or scrapes. While such evidence can be useful for basic studies, using remotely-triggered camera traps offer researchers more reliable evidence of animal presence and, with appropriate study design and analysis, provides an array of opportunities to investigate carnivore ecology. We present an overview on camera trap uses for the study and conservation of wildlife, with a particular focus on tropical carnivores. Our goals are to promote proper and effective application of camera trapping and related analyses. We highlight major research avenues, give relevant examples and lessons learned from published material and from our own experiences, and review available resources for implementation, from preparation and camera trap field set up, to data management, analysis, and presentation of results. Our review considers sampling design with respect to target species or groups of species, the state variable(s) of interest, what constitutes a sample, sample size needed, collection of supporting data (independent variables), reducing bias/minimising error, and data collection schedule. We also highlight some available camera trap database management packages and available statistical packages to analyse camera trapping data. We discuss presenting findings to a wider audience so results become useful in the conservation and management of species. Finally, we discuss future development of camera trapping technology and related techniques for the study and conservation of carnivores in the tropics.

KEY WORDS. — camera trapping review, elusive carnivores, photographic sampling, predator, wildlife research in the tropics

INTRODUCTION

Tropical carnivore ecologists often receive questions about the number of times they have directly observed the animals they study in the wild. Typically, the answer to such questions is "hardly ever" or "never". Past studies on tropical carnivores and many other secretive animals relied on indirect evidence of animal presence such as tracks, scats, or scrapes, which can be useful for simple distribution mapping. However, relatively recent techniques using camera traps offer researchers more reliable evidence of animal presence. Moreover, standardising effort and sampling protocol is relatively easy to do in camera trapping; and there is plenty

of room for improvement in the study design and analysis, allowing more thorough investigation of carnivore ecology.

Tropical rainforest carnivores have characteristics that make camera traps an ideal study tool. These characteristics include their body size (medium or large), morphology (natural marks for individual identification), guild/habitat in which they live (terrestrial—allowing for relatively simple placement of equipment), behaviour (readily use trails), secretiveness/elusiveness (difficult to study with other methods; Griffiths & Schaick, 1993; Karanth et al., 2004b), rarity (requiring large survey effort; Goldman & Winther-Hansen, 2003; Wibisono & Mccarthy, 2010), activity patterns (often nocturnal and

challenging for direct observation), and generally remote locations, which make long-term studies, direct observations, and field work extremely expensive or unfeasible.

Compared to tracks or scat, pictures from camera traps are superior in that they allow animal identification and verification in a relatively straightforward manner and with minimum ambiguity. Once they are set up, camera traps can accumulate efforts quickly over large areas. Additionally, camera traps can record information such as the date and time of the photograph, temperature, and location, either directly stamped on each picture, recorded as image file properties, or noted on a related datasheet. Other supporting information can also be collected including data related to location (GPS coordinates, terrain, slope, altitude, habitat/cover type), time (climatic parameters such as temperature, rainfall, humidity, etc.), or survey effort (number of trap nights, personnel involved, ad hoc/systematic, etc.).

For studying certain taxa and for certain purposes, camera trapping is often superior to other survey methods: For example, in species inventories, camera trapping proved to perform better than interviews (Can & Togan, 2009), scat collection (Davison et al., 2002; Weckel et al., 2006), track plot/plates (Foresman & Pearson, 1998; Wolf et al., 2003; Lyra-Jorge et al., 2008), or direct observation/count (Griffiths & Schaick, 1993; Silveira et al., 2003). It can also provide better data to investigate activity patterns than radio telemetry (Bridges et al., 2004b) and has the additional advantage of being non-invasive. The technique is especially popular for estimating abundance in individually identifiable species (e.g., Karanth & Nichols, 1998).

Though advantageous in many aspects, camera trapping cannot be considered a silver bullet to studying carnivore ecology (e.g., Gompper et al., 2006). For some objectives and conditions, there are other techniques that work better. For example, although camera traps might be used to obtain estimates of minimum home ranges in individually identifiable species (e.g., Franklin et al., 1999), radio or GPS telemetry would be a better approach. In spite of these limitations, camera traps offer many possibilities in wildlife research.

OBJECTIVES AND SCOPE

Our goals are to promote proper applications of camera trapping techniques and to increase the effectiveness of the applications to achieve different objectives in the study and conservation of tropical carnivores. With this both regional and taxonomic focus, this review represents a more specific addition to existing texts and books dedicated to camera trapping (e.g., Rovero et al., 2010; O'Connell et al., 2011a). Against this background we present relevant examples and lessons learned from published material and our own experience, discuss major research avenues and data analysis procedures, highlight study design and available resources for study implementation from preparation and field set up to data management, analysis, and presentation of results.

We limit our interpretation of camera traps to those "remotely triggered cameras that automatically take images of whatever walks in front of them" (Rovero et al., 2010: 102). There are similar systems that are potentially useful to study wild carnivores in the tropics but they are not the focus of this review. Examples of such systems are non-triggered camera traps programmed to periodically record images at certain times (Cutler & Swann, 1999), spy cameras designed to follow an animal (e.g., http://www.bbc.co.uk/news/science-environment-12070732), surveillance (video) cameras that are continuously recording events, or cameras attached to animals to observe surroundings (e.g., http://boingboing. net/2007/06/06/cat-has-camera-on-co.html). Although we focus on the use of still images, we also consider video camera traps that record motion pictures with or without sound.

In this paper, we briefly describe the evolution of camera trapping techniques, give examples of the equipment used to study a variety of animal taxa, and explain some technical aspects of the most commonly used camera trap models, including set up. We also discuss preparation of camera trapping studies, data management and analysis, and presentation of results. To support the text, in an online supplement we present some resources that can be useful to help design and implement effective camera trapping studies for tropical carnivores.

THE EVOLUTION OF CAMERA TRAP APPLICATIONS

Camera traps were initially developed mainly for aesthetic purposes (Guggisberg, 1977; Sanderson & Trolle, 2005). One of the first quantitative ecological studies that used camera traps was carried out by Pearson (1959) to investigate habitat use and activity patterns of small animals, including mice and lizards. The wider uses of camera traps as a surveillance tool by hunters in the late 1980s (Kays & Slauson, 2008) is the main reason they became commercially available and why technology rapidly developed. Use of camera traps in ecological research has boomed since the last decade (Rovero et al., 2010; O'Connell et al., 2011b) following the successful combination of camera traps with rigorous statistical analyses (Griffith & van Schaik, 1993; Mace et al., 1994; Karanth, 1995; Karanth & Nichols, 1998). Camera traps have become an indispensable tool in many wildlife studies worldwide ranging from simple documentation of animal presence to rigorous investigation of animal ecology based on quantitative, experimental and statistical inference. Kucera & Barrett (2011) provide a more detailed account of the history of camera trap development.

Today, camera traps are typically used to investigate medium to large terrestrial mammals (Griffiths & Schaick, 1993; Kays & Slauson, 2008). However, the equipment has also been applied successfully in studies of other groups of animal including small terrestrial mammals (Pearson, 1959), ground birds (O'Brien & Kinnaird, 2008), arboreal or scansorial mammals (Oliveira-Santos et al., 2008), and predators of avian nests (Goetz, 1981; Browder et al., 1995). The technique

is used in a variety of environmental conditions ranging from cold temperate, higher altitude areas (Jackson et al., 2006) to hot, humid tropical forests (Mohd-Azlan, 2009).

EQUIPMENT

There are a wide variety of camera trap models currently available, from ready-to-use units to those that require assemblage/development. As in general photography, camera trapping has almost entirely shifted from an analog/film to digital systems. Digital camera traps are superior in many aspects including instant result viewing, much better data storage capacity, more extensive metadata that comes with images, the ability to shoot videos, and wider availability of infrared flash. Some recent models of digital camera trap, integrated with communication networks such as cell or satellite phone, allow researchers to receive images taken by their camera units instantly on their phone or computer (e.g., http://www.alibaba.com/product-gs/389370506/gsm mms outdoor wireless hunting trail.html). On the other hand, analog camera systems, at least by the time this manuscript was being written, have a higher picture quality/resolution, faster trigger speed, and a wider availability of white flash. While infrared flash minimises disturbance to the animals, especially those exhibiting trap shyness (e.g., Wegge et al., 2004) it does not have the beneficial effect of freezing the movement of animals. Generally, pictures of animals taken in the dark using digital cameras with infrared flash are more susceptible to blurring. However, with recent technological development, some infrared cameras (e.g., Reconxy®) can take good pictures in the dark; and with proper camera placement and setting, the picture quality can be enhanced, increasing the prospect for individual identification of identifiable species.

Camera traps also vary in type of triggering mechanism. Originally, camera traps relied on physical triggering mechanisms such as pressure pads (Griffith, 1993; Griffiths & Schaick, 1993) or tripwires (Kucera & Barrett, 2011). Such mechanisms have some limitations with regard to the physical characteristics of the animal (such as body weight) that may cause the trigger to fail. Also, with physical triggers the target animal must be guided to a specific point in order to trigger the camera. Currently available camera traps mostly use either passive (PIR, e.g., http://en.wikipedia.org/wiki/ Passive infrared sensor) or active (AIR, e.g., http://www. trailmaster.com/tm1550.php) infrared motion detectors. Cameras with PIR sensors are more widely available and are generally easier to transport/install in the field because the camera, flash, sensor, and other accessories are all integrated in one self-contained unit. AIRs usually have separate components (e.g., the camera, transmitting, and receiving units) providing more flexibility in camera positioning relative to the target. Modifying components of AIRs is usually easier, including the use of better quality cameras such as digital single-lens reflex (DSLR) cameras. PIRs are only sensitive to objects with a different temperature from the ambient (with warm-blooded animals being the target) so that they can fail to record passing animals if ambient temperature is close to body temperature. On the other hand, AIRs can be triggered by anything including falling leaves or rain, causing a higher rate of false triggering (Swann et al., 2011), which is an issue particularly in the wet tropics.

The use of DSLR cameras overcomes several issues still strongly associated with many digital camera traps currently available. A quick trigger response, higher ISO and consequent higher shutter speed, and an overall higher image quality (mainly due to the larger size of the image sensor), among other features, make DSLR superior to point-and-shoot cameras. In addition, the option to interchange lenses allows researchers to modify DSLR-based camera-traps such as those from Nikon® or Canon® (check www.kenrockwell. com, for a review) to their particular needs. However, a DSLR camera is much more expensive, increasing equipment costs and considerable financial losses from theft. Also, their practicality for fieldwork is generally lower due to size, weight and the extra work needed to weatherproof and to assemble the necessary components.

In addition to the actual camera-trap, diverse equipment is needed to run a camera trapping study. We present an example list of camera trapping equipment in Appendix 1.

CAMERA TRAPS IN TROPICAL FORESTS

Every camera trapping study requires equipment that matches the study objectives, conditions of the study area, and the target animal(s). For tropical habitats, equipment must be able to withstand high heat and particularly, high humidity. Adding packets of desiccants inside the camera box helps protect the unit from extreme moisture, but these need to be replaced often. Frequent camera checking for cleaning and maintenance is necessary.

Habitats where tropical carnivores live are often remote and difficult to access. It may take several days of driving or boating to reach a village closest to the study area. From there, reaching actual field sites can require additional days of travel on foot. Therefore equipment weight is an important issue but should not override equipment quality. Smaller well-built cameras, although potentially pricey, may end up cheaper for the overall budget, especially where field logistics are extremely expensive. Using cheaper cameras that perform poorly may also make the ultimate costs soar and introduce bias into the data. Battery power must also be considered. It is best to use a widely available battery type with high durability. Rechargeable batteries can be efficient especially if they are high capacity NiMH. However, rechargeable batteries currently do not have nearly the same lifespan in the field as good quality non-rechargeable alkaline or lithium batteries, which allow for less frequent camera checks. Memory card size, which posed a dilemma until recently, is no longer an issue as capacity has tremendously increased while prices have declined. Swann et al. (2011) provide further information on types and features of camera traps and factors to consider in selecting the right equipment for different study conditions.

SURVEY DESIGN AND CONDUCT

Study objectives. — Two major factors usually motivate wildlife ecological research: pure scientific explorations or management/conservation. Camera traps can give insight into aspects of a species' behavior, such as activity patterns (van Schaik & Griffiths, 1996; Gomez et al., 2005; Oliveira-Santos et al., 2008; Linkie & Ridout, 2011), mating, breeding, foraging/hunting, denning (Bridges et al., 2004), or species interaction (Griffith & van Schaik, 1993; Linkie & Ridout, 2011; Sunarto, 2011; Sollmann et al., 2012).

In terms of species or population management and conservation, camera traps are usually employed to investigate one of two major issues: population parameters and parameters related to species occurrence or distribution (Kays & Slauson, 2008). Studies include documenting the presence of certain species in specific sites/areas (e.g., Brink et al. 2002), inventories of carnivore and prey diversity (O'Brien, 2008; Rovero et al., 2010), studying/mapping geographic distribution (e.g., Moruzzi et al., 2002a), modeling occupancy patterns and related habitat use/preferences (Linkie et al., 2007), population estimation (absolute or relative abundance and density; e.g., Rayan & Mohamad, 2009), including variation of these parameters across geographic locations or different habitat types (Kelly et al., 2008), and the investigation of population dynamics (including survival, immigration/emigration [Karanth et al., 2006; Gardner et al., 2010a]). Depending on the research objective, the study design, and setup, the data collected will vary. Because of the space limit, we do not discuss in great detail how camera trap sampling should be designed for each specific objective. Rather we present important general aspects to consider when designing camera trap sampling and refer the reader to more detailed literature.

Data collection. — Measures such as abundance or presence are also called state variables, because they describe the state of the studied system. The most basic approach is to use descriptive or summary variables to approximate state variables of interest. These include the number of individuals photographed, the number of (independent) pictures of the target species, sampling effort, and the photographic capture rates. These descriptive variables are very useful in identifying hotspots of high animal activity or in comparing effort and success across studies. Depending on the research question, these measures can be determined for the entire duration of a camera trap study, for sub-periods of time, across all camera trap units or separately for each unit. The most flexible scheme is to calculate these measures separately for each camera station, as the data can then be analysed at the camera station level or combined across the entire site. If the study is divided into temporal sub-periods, data can also be condensed to a binary detection/non-detection format (i.e., whether or not a species was detected in a given sub-period or not). We may be interested in investigating correlations between these measures with potential explanatory, or independent, variables. Examples of independent variables are those related to micro-habitat, macro-habitat, landscape features, and environmental/climatic, socio-economic and

anthropogenic factors. These variables also can be measured on a sampling unit (i.e., camera station) or a study area scale.

As a call for caution, the use of these raw descriptive variables such as a trapping rates as a surrogate for abundance does not account for the fact that our ability to observe individuals or species is imperfect, and that the probability of observing a species (or an individual of a given species) is unlikely to remain constant across species, space, and time (Link & Sauer, 1998; Pollock et al., 2002). Failure to account for imperfect detection can lead to biased results. Analytical approaches to account for imperfect detection are discussed in the data analysis section.

Sample unit and size. — The sample unit can vary with the study objectives. For example, in spatial terms a study using occupancy models might consider a habitat unit, an area/grid cell, or camera station as the sample unit, while on the temporal scale the sampling occasion could be the sample unit. Meanwhile, studies investigating animal activity might consider the trap day, each animal record, or each individual animal as their sample unit. When estimating abundance, the individuals detected are the sampling unit, but the number of times they are recaptured also determines whether the sample size is large or small.

Sample size needed depends on factors ranging from the degree of precision one aims to achieve, to the complexity of the analysis or the number of independent variables to use in analytical models. Further, the amount of data an investigator can actually collect will be limited by resources available or the nature of the target animal or area. Burnham & Anderson (2002) and Hines et al. (2010) provide further discussion on this issue.

STUDY SETUP

Selecting where and how to place cameras in the field is a crucial part of the project setup and deserves time and consideration on several levels:

Characteristics of target species. — Important factors to consider in designing camera trap sampling are the characteristics of the target species. First, consider whether or not the animal has natural marks for individual identification (and if so, what are the diagnostic characteristics). This will not only determine whether investigators can focus on analytical approaches that require individual-level data (e.g., capture-recapture models) or species-level data (e.g., occupancy models). It will also influence how to aim the camera's lens. Even species with little or no apparent natural marks might still be effectively identified individually if picture quality is sufficient so that researchers can distinguish morphological details of the animals (e.g., bobcats [Lynx rufus; Heilbrun et al., 2003], maned wolves, [Chrysocyon brachyurus; Trolle et al., 2007], pumas, [Puma concolor; Kelly et al., 2008], Javan rhino, [Rhinoceros sondaicus; Hariyadi et al., 2011]).

Second, the movement range of target species will determine how far apart traps should be spaced to achieve either independence of sampling units (a prerequisite for occupancy modeling) or to make sure all individuals in the sampled area are exposed to traps (an assumption of capture-recapture models).

Finally, for species occurring at very low densities, targeting specific landscape structures or habitat types used by these species may be the only means of collecting an adequate number of records (e.g., Karanth, 2011). Under these circumstances, any knowledge of preferences for certain landscape structures such as roads or rivers will be helpful in designing a camera trapping study.

When studying a single species, tailoring the study design to its characteristics may be relatively straight forward. However, when a study targets multiple species, for example in assessing carnivore diversity or interaction among species, it is important to ensure a study design that is balanced regarding the different target species. When analytical approaches do not account for differences in detection probability among species (see Analytical approaches below), it is imperative to evaluate or recognise the potential biases introduced into the data by a species-specific study design and extreme care should be taken in inference.

On a smaller scale, exactly where and how to set up camera traps at the sampling sites must be evaluated at various levels (for an example, see Fig. 1). Body size of the target species and the field of detection of the particular camera trap model will determine camera height and distance from the trail (Kelly & Holub, 2008, Tobler et al., 2008).

Camera trapping studies often have to be conducted when there is little or no available information on particular species. In this case, information on similar species or the same species from a better studied region can be useful.

Logistics and operational considerations. — In addition to the study objectives, researchers must consider operational conditions including security of cameras from various threats such as harsh weather/climate, direct sunlight (for cameras with passive sensors), human vandalism, and disturbance/ damage by organisms (including large and small animals, insects, plants, and fungi). Different techniques can be applied to address these factors. They include weather/waterproofing using desiccants to absorb moisture, armoring cameras with extra protection to prevent damage by large animals and people (e.g., Grassman Jr. et al., 2005), regular patrolling, talking directly to local leaders and/or adding persuasive notes on each camera to prevent vandalism. Regular checking of traps will help keep the study running smoothly in spite of such difficulties. While checking intervals will depend on camera trap model (battery life, picture storage capacity) and study site (high or low animal and human traffic, risk of camera disturbance, etc.) checking cameras every other week might be ideal as it balances between the need to ensure cameras are operational and to minimise the disturbance to the animals. In certain areas the use of camera traps may be completely unacceptable, such as in areas inhabited by

indigenous people who do not want their pictures taken (D. Priatna/ZSL, pers. comm.). Overall, the study should be designed so that frequent camera checks are feasible with the financial, logistical, and personnel resources available. These aspects must be assessed on a site-by-site basis. Unfortunately, there is no such thing as "one solution that fits all".

Data collection schedule. — Factors to consider in the data collection schedule include survey timing (time of year, month, seasons), single versus multiple repeated surveys (e.g., investigation of trends over time), duration of the survey, and how often cameras should/can be checked.

Logistically, some areas might be impossible to survey during the rainy season, due to heavy flooding, access difficulties, or increased danger of fieldwork. In other areas, the rainy season might be the only time areas can be accessed, for example, if boat transportation requires adequate water levels or if water supplies for drinking are only available during the rainy season. Another logistical consideration is whether local guides are needed and available during the

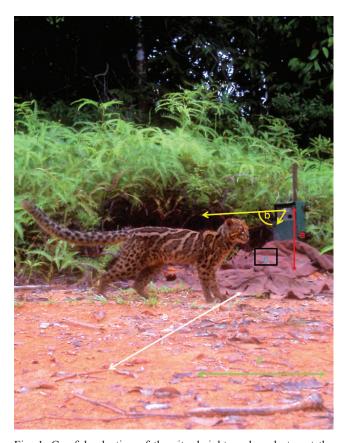


Fig. 1. Careful selection of the site, height, and angle to set the camera trap considering the characteristics of target animals is a key factor in determining the success of a camera trapping study. The present example shows a two-camera set-up for individual identification: a) height of 30–40 cm designed for small to medium-sized carnivores; b) camera angle that is not directly facing the other camera at the same station; c) pile of leaves to protect against splashing mud in heavy rain; d) placement along old logging road when applicable to increase the probability of detection; and e) vegetation clearing to ensure clear picture of the animal and avoid misfiring. (Photograph by: Wilting, Mohamed, Sabah Wildlife Department & Sabah Forestry Department).

survey. Anticipating holidays or farming seasons in villages helps to avoid time loss. Ecologically, investigators should anticipate that carnivores are likely to exhibit temporal/seasonal variation in numbers or behavior (Barlow et al., 2009). Investigators must sample all seasons if seasonal variation is the parameter of interest. For other objectives, there might be more flexible options such as sampling during the season when probability of capturing carnivores is the highest.

Any state variable estimated is only meaningful for the time frame in which it remains stable, i.e., in which the system under study is 'closed'. For example, if there is seasonal variation in habitat cover, the distribution of a species can change between seasons; or, in a situation where individuals may be born or die during sampling (i.e., open population), abundance would no longer be a meaningful measure. Therefore, it is important that sampling takes place within a time frame during which the parameter of interest is unlikely to change. With rare and elusive species, investigators usually need to compromise between sampling long enough to collect enough data, but short enough so that the parameter under investigation is biologically and ecologically meaningful. The actual amount of time depends on the biology of target species and study area. As an example, for big cats, a study duration of 2-3 months is generally deemed adequate to approximate a closed population (Henschel & Ray, 2003; Silver, 2004).

Reducing bias and error. — It is crucial to standardise the sampling technique across camera stations (and across repeated samples in space and time), unless variation in sampling technique is the factor of interest. When complete standardisation is not possible, the impact of differential sampling should be assessed and, if possible, minimised. For example, probability of detection can be influenced by the use of different camera trap brands/types/accessories, different settings (such as flash, delay time, ISO, aperture/ shutter speed), the use of bait/lure versus non bait (Hegglin et al., 2004; Gerber et al., 2012), trap placement on or off roads (Sollmann et al., 2011), a response to trapping (i.e., trap-happiness and trap shyness [Sequin et al., 2003; Wegge et al., 2004]), or change in detection over time and with season (Selmi & Boulinier, 2003; Tracey et al., 2005). Unless we use an analytical approach that adequately accounts for variable detection, results of our analyses will exhibit complex bias. Even when accounting for variation in detection, the more sources of variation the more complex our model and the more data we need.

Placement of camera traps at landscape features that are preferentially visited by a certain species (e.g., forest roads used by large cats; Karanth & Nichols, 1998) is recommended to increase the probability of detection. Such a setup targets a single species, but might not be optimal for other species in the study area. Additionally one portion of the population (males for example) may be more likely to be photographed on large roads. Investigators may unwittingly introduce errors into the data through careless selection of location to inappropriate camera settings.

Because of the wide range of conditions and dynamics of the study systems, a technique that works well for one species might not work for another. Even for the same species, the ideal setup may vary by habitat type or geographic location. Therefore, it is important to continuously evaluate and refine sampling techniques (Kelly, 2008).

MANAGING CAMERA TRAP DATA

Camera trapping investigators likely will spend a large amount of their time cataloging, managing, and analysing their photographic data. Therefore, it is important to spend adequate time thinking in advance about how camera trapping data should be stored and managed, and to plan extensive time for data entry.

Camera trap data contain a wide array of information, usually only part of which is used by the investigator. However, we advise entering photographic data on all non-target species including humans as this information can be extremely valuable to management or can serve as potential variables to predict the target species' presence or abundance. Not only are the data likely to be useful to examine inter-specific-interactions or impacts of human use, but a complete database will also make later analyses much easier, as researchers will not have to slog back to the original photographs. Further, a complete database enhances the ability to compare across sites or share data and contribute information to other projects interested in different species.

Other types of information that should be recorded with a camera survey include: name of study area and its management status and habitat type, survey name, time and duration, geographic coordinates of each trap, and type of cameras and settings used. We also advise recording species, sex, individual (if possible), age category, number of animals, time and date of record, camera number, and image number. Raw data tables may form the base for derived, analysis-specific data tables, for example, individual detection/non-detection matrices (X-matrix) for capture-recapture models (see analysis section below). Relational databases, where different tables are connected/related using key fields allowing multiple tables to be queried at once to generate/derive new table or information, are useful to efficiently manage camera trapping data.

Investigators can either develop their own camera trap database using a spreadsheet application such as Microsoft Excel or Microsoft Access (see Appendix 5 for example spread sheet for entering raw data), or use a database already developed and made available by others. Examples of existing databases specifically formatted to manage camera trapping data include Camera Base, http://www.atrium-biodiversity.org/tools/camerabase/ (Tobler, 2010), WWF-Malaysia Camera-Trap Database (http://myrimba.org/2012/01/05/toolbox_update_5/), and an even more recently released database by Harris et al. (2010) and Sundaresan et al. (2011).

DATA ANALYSIS

Due to space limitations we are unable to provide a comprehensive overview of analytical approaches used with camera trapping data, but refer readers to the recent book by O'Connell et al. (2011) for a comprehensive review. Instead, we highlight popular analytical applications of camera trapping data, organised according to the objective of the study.

Species inventory. — The most basic information camera trapping can provide is a list of medium and large sized mammal species in the study area—a species inventory (Lorenzana Pina et al., 2004; Azad, 2006; Azlan & Sharma, 2006). Rovero et al. (2010) provide a detailed manual on the use of camera traps for the inventory of terrestrial vertebrates and several authors have evaluated and discussed camera trapping for wildlife inventories (Silveira et al., 2003).

The failure to photograph a species should never simply be mistaken for a proof of absence of the respective species (e.g., MacKenzie, 2005). Very rare or elusive species, or species with specific behavioral traits such as arboreal or aquatic habits, can be missed completely by camera traps even with considerable sampling effort. To achieve a more reliable "absence record", a researcher can estimate the amount of effort needed to detect the species at least once based on a 'guesstimated' density (Carbone et al., 2001) or the detection probability documented in other places or for other similar species. This has been applied to clouded leopards in Taiwan and to tigers (Panthera tigris) in South China (Tilson et al., 2004; Chiang, 2007; Sanderson, 2009). However, absence records should be interpreted with caution, since the probability to detect a species likely varies with the study site and time (Royle & Nichols, 2003; Mackenzie et al., 2006).

Using species accumulation curves (Colwell et al., 2004) or capture-recapture based approaches (Boulinier et al., 1998) can aid species inventories by accounting for species not recorded in camera surveys. Free software tools, such as Estimates (http://viceroy.eeb.uconn.edu/estimates), can be used for camera trapping data to investigate issues of species richness.

Species distribution and occupancy. — With extensive placement of the equipment across a geographic region of interest, camera traps are very useful to investigate carnivore distribution (Moruzzi et al., 2002b). For example, Pettorelli et al. (2010) combined camera trap surveys across 11 sites in Tanzania, East Africa with ecological niche factor analysis (ENFA) to reveal distributional and habitat use patterns for seven elusive carnivores simultaneously. However, this approach does not explicitly model detectability.

With proper sampling design, data from camera trapping are suitable for analyses using occupancy models (MacKenzie et al., 2006). This approach has a wide array of applications to estimate parameters related to species occurrence, such as the percentage of an area occupied by a species (PAO), the

probability of species occurrence at a site, and parameters related to changes in occupancy over time, such as the probability of local extinction or re-colonisation (MacKenzie et al., 2006).

In occupancy modeling, the sample unit generally consists of an area, such as a distinct habitat unit (or fragment), plot or grid cell, defined by the investigator. Sampling units should be spatially independent, meaning they should be sufficiently spaced such that a given individual will only be present at a single sample unit (for a detailed account on occupancy study design, please consult MacKenzie & Royle, 2005; MacKenzie et al., 2006; Guillera-Arroita et al., 2010; Hines et al., 2010). The estimated probability of occupancy refers to the entire sampling unit, and researchers may want to deploy several camera traps in a single unit to achieve better spatial coverage. This approach also can be used to investigate aspects such as habitat associations (Sunarto et al., 2013) or species interaction (Sunarto, 2011).

Favorable features of occupancy models include: 1) they fully account for imperfect species detection and varying detection probabilities among species, sites, time intervals etc.; and 2) they tolerate missing sampling occasions without affecting the parameter estimates (Hines, 2006). A combination of these features and the rapid development of the method and availability of related infrastructure (e.g., software to implement the analysis, guidebook, and expert support) have facilitated the adoption of the approach in recent camera trapping studies (e.g., Linkie et al., 2007; O'Brien & Kinnaird, 2008; Tobler et al., 2009). These models can be implemented in the R package "unmarked" (Fiske et al., 2011), in a Bayesian framework (Royle & Dorazio, 2008) using WinBUGS (Gilks et al., 1994), or in the specific programs PRESENCE (Hines, 2006) or MARK (White, 2009).

Other statistical procedures can be used with camera trap data such as logistic regression (Hosmer & Lemeshow, 1989), log-normal (Poisson) regressions, negative binomial regression or other generalised linear models, to analyse camera trapping data to reveal resource selection functions, habitat use or selection (Manly et al., 2002; Keating & Cherry, 2004), distribution prediction (Linkie et al., 2006; Karanth et al., 2009), and species interactions (Weckel et al., 2006; Davis et al., 2010; Linkie & Ridout, 2011; Sunarto, 2011). However, some of these examples do not take imperfect detection into account, which can potentially distort inference (MacKenzie et al., 2005).

Population abundance and density. — One of the most common objectives of camera trapping is to estimate the size and/or density of a population in a given area. Camera trapping in combination with capture-recapture (CR) models has proven useful not only for large carnivores with conspicuous individual marks such as the tiger (Karanth, 1995; Karanth & Nichols, 1998; O'Brien et al., 2003), jaguar (Panthera onca; Silver et al., 2004), leopard (Panthera pardus; Balme et al., 2010), and Sunda clouded leopard (Neofelis diardi; Wilting et al., 2012), but also for smaller

carnivores like ocelots (*Leopardus pardalis*; Dillon, 2005), leopard cat (*Prionailurus bengalensis*; Mohamed et al., 2013) or civets and mongooses (Gerber et al., 2010), and species without immediately conspicuous individual markings such as pumas (Kelly et al., 2008; Negrões et al., 2010) or maned wolves (Trolle et al., 2007).

Using CR models to estimate abundance from individual detection/non-detection data has a long history (Otis et al., 1978; Chao & Huggins, 2005). Use of such models in combination with camera trapping data began in the mid-1990s and has greatly enhanced our understanding of carnivore population status over the last two decades (Karanth & Nichols, 1998; O'Brien et al., 2003; Trolle & Kery, 2003, 2005; Karanth et al., 2004a; Maffei et al., 2004; Silver et al., 2004; Dillon, 2005; Jackson et al., 2006; Martins & Martins, 2006; Soisalo & Cavalcanti, 2006; Hutajulu et al., 2007; Hebeisen et al., 2008; Gerber et al., 2010). CR models can be implemented in well-established software packages such as Program CAPTURE (Rexstad & Burnham, 1992) or Program MARK (White, 2009). In addition to estimating the size of so-called closed populations, these models can also handle parameters describing the dynamics of open populations, such as survival or recruitment rates (Amstrup et al., 2005; Karanth et al., 2006).

Although CR models provide a statistically sound means of estimating abundance, deriving a density estimate is problematic. Animal movement on and off the sampling grid violates the assumption of geographic population closure (Kendall & Nichols, 1995; Kendall et al., 1997) and also means that the abundance estimate refers to an area that is larger than the polygon delineated by the outermost traps. The standard approach is to buffer the trap polygon with half the mean maximum linear distance moved by individuals captured in more than one trap (MMDM; Karanth & Nichols, 1998) and use this buffered area, the effective sampled area, to estimate density by dividing abundance by this area. Other approaches that have been used to estimate buffer width include the full MMDM, or the radius of an average home range based on telemetry data (Soisalo & Cavalcanti, 2006) or on information from the literature (Wallace et al., 2003). Although some approaches performed well in simulation studies (Wilson & Anderson, 1985), they are ad hoc approaches with little theoretical justification (Williams et al., 2002). Since density estimates are heavily influenced by the chosen buffer width, comparison of estimates from studies determining the buffer width in different ways becomes problematic. In addition, trap spacing and the size of the overall trapping grid relative to animal movement influence density estimates (Bondrup-Nielsen, 1983; Dillon & Kelly, 2007, 2008; Maffei & Noss, 2008). Latest developments, therefore, have focused on minimising such drawbacks.

A recent analytic development is spatial capture-recapture (SCR) modeling. These models have two major advantages over traditional CR models: 1) They make use of the spatial information of individual captures to model individual movement and account for differential exposure of individuals to the trapping grid, thereby addressing a major source of

individual heterogeneity in detection probability; 2) By treating the trapping grid as embedded in a larger area, they circumvent the problem of estimating an effective sampled area (Efford, 2004; Royle & Young, 2008).

This approach can be implemented using either maximum likelihood estimation techniques in Program DENSITY (Efford, 2010) or the equivalent R package secr (Efford, 2011), or in a Bayesian framework (Royle & Gardner, 2011) in Program WinBUGS (Gilks et al., 1994) or the R package SPACECAP (Singh et al., 2010). These approaches provide a flexible framework where both trap station specific and individual covariates can be included in the models (Gardner et al., 2010b, Kery et al., 2010). Models can be expanded to handle open populations, allowing the estimation of demographic parameters such as survival and recruitment (Gardner et al., 2010b). In comparison to non-spatial CR models, SCR models often result in lower estimates of density (Tredick & Vaughan, 2009; Sharma et al., 2010; Gerber et al., 2012; Sunarto et al., 2013). This is probably a result of these models more fully accounting for animal movement off the trapping grid, which is most likely underestimated by the ad hoc approach to animal movement (Bondrup-Nielsen, 1983).

Abundance estimation when individuals cannot be distinguished. — Any type of capture-recapture analysis requires individual-level data and, thus, that individuals can be distinguished based on camera trap pictures. Obviously, this is not possible for a wide range of species, including many carnivores. There are two alternative model-based approaches towards this estimation problem: Rowcliffe et al. (2008) formulated a model under which density is essentially a function of the trap encounter rate and animal movement speed and activity. Apart from the fact that reliable estimates of movement speed may be difficult to obtain, the model also requires a camera trap setup that is random with regard to animal movement (i.e., targeting landscape structures with known higher animal traffic is not allowed), which may be difficult to implement in study areas with limited access and, for rare species, may result in prohibitively low amounts of data. The second approach is essentially a variation of an occupancy model, under which the probability of detecting a species in a sampling unit is related to the species' abundance in that unit (Royle & Nichols, 2003). However, converting these point estimates of abundance into a meaningful estimate of overall abundance for a study site or translating them into a density estimate can be difficult.

A third approach is the use of abundance indices, usually some variation of the number of photographs of the focal species per trap day (O'Brien, 2011). When used to estimate absolute abundance or density, such an index requires an independent estimate of density for calibration (Carbone et al., 2001). The usefulness of this approach has been questioned as the relation between the index and true density is unlikely to be constant across sites, species or time (Jennelle et al., 2002). More often, camera trapping data is used to derive relative abundance indices (RAI; e.g., O'Brien et al., 2003) for example, to investigate relative abundance of prey species

in studies of carnivore feeding ecology (Weckel et al., 2006; Cavalcanti & Gese, 2010). Without calibration, however, their comparison across time, space or species is extremely problematic (O'Brien, 2011). Such comparisons are based on the assumption that detection probability is constant across these dimensions, which, as previously discussed, is improbable. As a consequence, the use of RAIs can lead to erroneous conclusions about the abundance of species. Such indices should only be used as a measure of trapping success or activity rates, not as a measure of abundance, unless there is strong evidence (which should be stated explicitly) that the assumption about constant detection probability is reasonable.

Activity patterns and other aspects of behavior. — The time of day a record was taken provides valuable information on the activity patterns of species. Different approaches can be implemented to analyse such data (e.g., van Schaik & Griffiths, 1996; Gomez et al., 2005; Azlan & Sharma, 2006; Cuellar et al., 2006; Ridout & Linkie, 2009). One of the simplest ways is to present the number or percentage of pictures for certain time interval in a 24-h period (van Schaik & Griffiths, 1996; Cheyne & Macdonald, 2011). The latest and more appropriate approach to analyse activity data is by considering the time of day as 'circular' (Fisher, 1993). Using modeling techniques such as kernel density estimation (KDR), activity patterns of different animals in the same study area can be compared to investigate possible interactions (Ridout & Linkie, 2009; Gerber, 2010; Linkie & Ridout, 2011; Sunarto, 2011).

Though not usually applicable for detailed behavioral studies in carnivores, camera traps can document certain aspects of animal behavior, including scavenging (Bauer et al., 2005), breeding (Cain Iii et al., 2003), denning behavior (Bridges et al., 2004), handling of prey items, females with offspring, scent-marking, use of water holes, and even some unusual behaviors (e.g., http://www.bbcwildlifemagazine.com/gallery/camera-trap-photo-year-2010-winners; Sanderson & Trolle, 2005).

Biodiversity monitoring. — With camera trapping it is fairly easy to standardise sampling to a large degree by using the same camera trap model, programming and setup throughout the study area and in repeated samples. This feature makes camera traps an ideal monitoring tool. Not surprisingly, therefore, some developments have been made toward the implementation of camera trapping for biodiversity monitoring (particularly those employing repeated sampling over relatively long time period) at various scales based on certain indicators such as presence and occupancy of mammals (Ahumada et al., 2011), the composition of the mammalian community (Sanderson & Trolle, 2005; Martins et al., 2007), or top trophic level species (O'Brien et al., 2010). They aim to assess impacts of more specific management actions such as removal of anthropogenic disturbance (Harihar et al., 2009) or conflict mitigation (Mohd. Azlan & Sharma, 2003), to assess the impacts of environmental variation (Wong et al., 2005), to assess the prevention of disease spread (Wolf et al., 2003), or to define conservation status of certain species (Kawanishi & Sunquist, 2004).

PRESENTATIONS OF RESULTS BEYOND RESEARCH

To have an impact and ultimately contribute to conservation and management, research must be disseminated. Unlike most of other research techniques that require some analysis to reveal ecological processes and patterns before the data become useful, camera trapping has the advantage that the raw material, i.e., the pictures themselves, can generate powerful information and are an invaluable tool for public awareness/advocacy. Photographs provide the public with immediate access to scientific works, much more so than any sophisticated statistics or graphs. Thus, presenting ongoing findings from the field as a news release or popular presentation can be an important contribution to raise awareness for urgent management issues. From central Sumatra, for example, awareness of tiger conservation has been successfully generated through press releases of camera trap photographs of a three-legged tiger, a victim of illegal snares set by poachers (e.g., http://www.reuters.com/ article/idUSJAK27242520070706), an adult tiger with cubs (e.g., http://wwf.panda.org/what_we_do/endangered_species/ tigers/tiger_films/tiger_cubs/), a bulldozer passing on a tiger trail (http://www.msnbc.msn.com/id/39651483/ns/ world_news-world_environment/), and more recently the possible impact of rapid forest conversion to plantation on the tiger population (http://news.mongabay.com/2011/0514google_earth_sumatra.html).

Pictures and data from camera traps have also been extensively used to support efforts to protect important wildlife habitats including Batang Gadis National Park in North Sumatra (Sunarto et al., 2004) and Tesso Nilo National Park in Central Sumatra (Departemen Kehutanan, 2009). In addition, camera traps can provide information useful to advocate better protection of habitats harboring rare or endangered species, as in the case of the rediscovery or new species records from camera trapping. For example, camera traps in the Malaysian state of Sabah on Borneo rediscovered the world's most threatened otter species—the hairy-nosed otter (*Lutra sumatrana*) after over 100 years (National Geographic Daily News).

Particularly for the case of tigers, camera trapping studies have become the key source of information to determine the conservation status (Chundawat et al., 2008; Linkie et al., 2008) and to formulate the conservation strategy both at the global (Global Tiger Initiative, 2010) and country levels (e.g., Soehartono et al., 2007).

FUTURE DEVELOPMENT

The last few years have seen massive progress in camera trap development. Design-wise, cameras are becoming smaller in

size and lighter in weight, while image quality is increasing; settings are becoming more flexible, batteries more efficient and operational life longer, which can ultimately makes camera trapping more environmentally friendly. Simultaneously, camera traps are becoming cheaper. With such developments, it is likely that camera traps will become more integrated with other data loggers to record more detailed biological, climatic, or environmental parameters.

The ability of digital camera traps to capture video sequences or take sequential pictures will promote further development. For example, video footage allows estimation of animal movement speed, which would facilitate the use of the gas model approach towards estimating density of animals where individuals cannot be distinguished (Rowcliffe et al., 2008). Another potential development is the use of three-dimensional imaging with multi-lenses (Moynihan, 2010). Technically, it should be possible to develop one camera with multiple lenses, connected to the camera wirelessly, allowing a single camera to capture images of an animal from different angles at the same time. Such advances not only will make fieldwork more efficient, but also will aid in identification of species, individuals, and/or physiological condition.

Technological advances related to the camera trap sensors have been widely applied in the gaming world, allowing the human body to be scanned, movements recorded, and analysed (e.g., www.xbox.com). Similar technologies in combination with the existing database and software might enable future camera traps to, for example, automatically identify species, individuals, gender; measure body mass, describe general physiological condition, and characterise movement. Eventually such new technologies will become more accessible and economical.

The last few years have also seen the development in camera-trapping related software for data management (Harris et al., 2010; Tobler, 2010), including individual identification (Kelly, 2001, Hiby et al., 2009), and analytical software (Hines, 2006; Ridout & Linkie, 2009; Efford, 2010; Singh et al., 2010; Sundaresan et al., 2011). Simultaneously, new analytical approaches are constantly being developed or existing approaches extended—as the relatively recent appearance of spatially explicit capture-recapture models demonstrates.

However, all of these advances will not automatically make camera trapping more efficient in the study and conservation of tropical carnivores. In fact, the effectiveness of camera trapping will rest largely on the shoulders and in the hands of the investigators and technicians who use them. We hope this review clarifies concepts, stimulates ideas, and provides guidelines to more efficiently design camera trapping studies in the future.

RESOURCES

To support the text, in this supplement we present some resources that can be useful to help design and implement an effective camera trapping studies for tropical carnivores including: 1) A list of equipment needed for a camera trapping study (Appendix 1); 2) Examples of datasheets for camera trap set-up (Appendix 2) and camera trap checking (Appendix 3); 3) An example of individual identification database (Appendix 4); 4) An example of data entry spread sheet for raw photo data with two cameras per station (Appendix 5); A brief decision guide to study design and data analysis for common purposes of camera trapping (Appendix 6).

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LITERATURE CITED

- Ahumada, J. A., C. E. F. Silva, K. Gajapersad, C. Hallam, J. Hurtado, E. Martin, A. McWilliam, B. Mugerwa, T. O'Brien, F. Rovero, D. Sheil, W. R. Spironello, N. Winarni & S. J. Andelman, 2011. Community structure and diversity of tropical forest mammals: Data from a global camera trap network. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **366**: 2703–2711.
- Amstrup, S. C., T. L. McDonald & B. F. J. Manly, 2005. *Handbook of Capture-Recapture Analysis*. Princeton University Press, Princeton, USA. 313 pp.
- Azad, M. A. J. B. A. G., 2006. Mammal diversity and conservation in a secondary forest in Peninsular Malaysia. *Biodiversity and Conservation*, **15**: 1013–1025.
- Azlan, J. M. & D. S. K. Sharma, 2006. The diversity and activity patterns of wild felids in a secondary forest in Peninsular Malaysia. *Oryx*, **40**: 36–41.
- Balme, G. A., R. Slotow & L. T. B. Hunter, 2010. Edge effects and the impact of non-protected areas in carnivore conservation: Leopards in the Phinda-Mkhuze Complex, South Africa. *Animal Conservation*, **13**: 315–323.
- Barlow, A. C. D., C. Mcdougal, J. L. D. Smith, B. Gurung, S. R. Bhatta, S. Kumal, B. Mahato & D. B. Tamang, 2009. Temporal variation in tiger (*Panthera tigris*) populations and its implications for monitoring. *Journal of Mammalogy*, 90: 472–478.
- Bauer, J. W., K. A. Logan, L. L. Sweanor & W. M. Boyce, 2005. Scavenging behavior in puma. Southwestern Naturalist, 50: 466–471.
- Bondrup-Nielsen, S., 1983. Density estimation as a function of live-trapping grid and home range size. *Canadian Journal of Zoology*, **61**: 2361–2365.
- Boulinier, T., J. D. Nichols, J. R. Sauer, J. E. Hines & K. H. Pollock, 1998. Estimating species richness: The importance of heterogeneity in species detectability. *Ecology*, 79: 1018–1028.
- Bridges, A. S., J. A. Fox, C. Olfenbuttel & M. B. Vaughan, 2004. American black bear denning behavior: Observations and applications using remote photography. Wildlife Society Bulletin. 32: 188–193.
- Brink, H., J. E. Topp-Jorgensen, A. R. Marshall & E. Fanning, 2002. First record in 68 years of Lowe's servaline genet. *Oryx*, 36: 324–324.

- Browder, R. G., R. C. Browder & G. C. Garman, 1995. An inexpensive and automatic multiple-exposure photographic system. *Journal of Field Ornithology*, **66**: 37–43.
- Burnham, K. P. & D. R. Anderson, 2002. *Model Selection and Multimodel Inference*. 2nd Edition. Springer, New York, USA. 488 pp.
- Cain Iii, J. W., M. L. Morrison & H. L. Bombay, 2003. Predator activity and nest success of willow flycatchers and yellow warblers. *Journal of Wildlife Management*, 67: 600–610.
- Can, Ö. E & İ. Togan, 2009. Camera trapping of large mammals in Yenice Forest, Turkey: Local information versus camera traps. *Oryx*, **43**: 427–430.
- Carbone, C., T. Coulson, S. Christie, K. Conforti, J. Seidensticker, N. Franklin, R. Tilson, J. R. Ginsberg, M. Kinnaird, R. Laidlaw, A. Lynam, T. O'Brien, W. N. Wan Shahruddin, M. Griffiths, J. Holden, D. Martyr, K. Kawanishi, M. Sunquist, D. W. Macdonald, L. Nath, C. McDougal & D. J. L. Smith, 2001. The use of photographic rates to estimate densities of tigers and other cryptic mammals. *Animal Conservation*, 4: 75–79.
- Cavalcanti, S. & E. M. Gese, 2010. Kill rates and predation patterns of jaguars (*Panthera onca*) in the southern Pantanal, Brazil. *Journal of Mammalogy*, **91**: 722–736.
- Chao, A. & R. M. Huggins, 2005. Modern closed-population capture-recapture models. In: S. C. Amstrup, T. L. McDonald & B.
 F. J. Manly (eds.), *Handbook of Capture-Recapture Analysis*.
 Princeton University Press, Princeton, USA. Pp. 58–87.
- Cheyne, S. M. & D. W. Macdonald, 2011. Wild felid diversity and activity patterns in Sabangau peat-swamp forest, Indonesian Borneo. *Oryx*, **45**: 119–124.
- Chiang, P.-J., 2007. Ecology and Conservation of Formosan Clouded Leopard, Its Prey, and Other Sympatric Carnivores in Southern Taiwan. Unpublished PhD Thesis, Virginia Tech, Blacksburg, USA. 250 pp.
- Chundawat, R. S., B. Habib, U. K. Karanth, K. Kawanishi, J. Ahmad Khan, T. Lynam, D. Miquelle, P. Nyhus, Sunarto, R. Tilson & S. Wang, 2008. *Panthera tigris* In: IUCN 2013. *IUCN Red List of Threatened Species. Version 2013.1* http://www.iucnredlist.org/details/15955/0.
- Colwell, R. K., C. X. Mao & J. Chang, 2004. Interpolating, extrapolating, and comparing incidence-based species accumulation curves. *Ecology*, 85: 2717–2727.
- Colwell, R. K., and J. A. Coddington, 1994. Estimating terrestrial biodiversity through extrapolation. *Philosophical Transactions of the Royal Society of London Series B: Biological Sciences*, **345**(1311): 101–118.
- Cuellar, E., L. Maffei, R. Arispe & A. Noss, 2006. Geoffroy's cats at the northern limit of their range: Activity patterns and density estimates from camera trapping in Bolivian dry forests. Studies on Neotropical Fauna and Environment, 41: 169–177.
- Cutler, T. L. & D. E. Swann, 1999. Using remote photography in wildlife ecology: A review. Wildlife Society Bulletin, 27: 571–581.
- Davis, M. L., M. J. Kelly & D. F. Stauffer, 2010. Carnivore coexistence and habitat use in the Mountain Pine Ridge Forest Reserve, Belize. *Animal Conservation*, 2010: 1–10.
- Davison, A., J. D. S. Birks, R. C. Brookes, T. C. Braithwaite & J. E. Messenger, 2002. On the origin of faeces: Morphological versus molecular methods for surveying rare carnivores from their scats. *Journal of Zoology*, 257: 141–143.
- Departemen Kehutanan, 2009. Keputusan Menteri Kehutanan Republik Indonesia tentang perubahan fungsi sebagian

- kawasan Hutan Produksi Terbatas kelompok hutan Tesso Nilo. *Keputusan Menteri Kehutanan Nomor: Sk. 255/Menhut-Ii/2004*. Departemen Kehutanan, Jakarta, Indonesia.
- Dillon, A. 2005. Ocelot Density and Home Range in Belize, Central America: Camera-Trapping and Radio Telemetry.
 Unpublished Masters Thesis, Virginia Polytechnic Institute and State University, Blacksburg, USA. 136 pp.
- Dillon, A. & M. J. Kelly, 2007. Ocelot *Leopardus pardalis* in Belize: The impact of trap spacing and distance moved on density estimates. *Oryx*, **41**: 469–477.
- Dillon, A. & M. J. Kelly, 2008. Ocelot home range, overlap and density: Comparing radio telemetry with camera trapping. *Journal of Zoology*, 275: 391–398.
- Efford, M., 2004. Density estimation in live-trapping studies. *Oikos*, **106**: 598–610.
- Efford, M., 2010. *Density 4.4: Spatially Explicit Capture-Recapture*. University of Otago, Dunedin, New Zealand.
- Efford, M. G., 2011. secr: Spatially explicit capture-recapture models. In: R Development Core Team, R Package. 2.0.0. Edition. R Foundation for Statistical Computing, Vienna, Austria.
- Fisher, N. I., 1993. *Statistical Analysis of Circular Data*. Cambridge University Press, Cambridge, UK. 296 pp.
- Fiske, I., R. Chandler & A. Royle, 2011. Unmarked: Models for data from unmarked animals. In: R Development Core Team (ed.), *R Package. 2.0.0. Edition*. R Foundation for Statistical Computing, Vienna, Austria.
- Foresman, K. R. & D. E. Pearson, 1998. Comparison of proposed survey procedures for detection of forest carnivores. *Journal of Wildlife Management*, **62**: 1217–1226.
- Foster, R. J., B. J. Harmsen & C. P. Doncaster, 2010. Habitat use by sympatric jaguars and pumas across a gradient of human disturbance in Belize. *Biotropica*, **42**: 724–731
- Franklin, N., Bastoni, Sriyanto, D. Siswomartono, J. Manansang & R. Tilson, 1999. Last of the Indonesian tigers: A cause for optimism. In: Seidensticker, J., S. Christie & P. Jackson (eds.), Riding the Tiger, Tiger Conservation in Human-Dominated Landscapes. Cambridge University Press, Cambridge, UK. Pp. 130–147.
- Gardner, B., J. Reppucci, M. Lucherini & J. A. Royle, 2010a. Spatially explicit inference for open populations: Estimating demographic parameters from camera-trap studies. *Ecology*, 91: 3376–3383.
- Gardner, B., J. A. Royle, M. T. Wegan, R. E. Rainbolt & P. D. Curtis, 2010b. Estimating black bear density using DNA data from hair snares. *Journal of Wildlife Management*, 74: 318–325.
- Gerber, B., S. M. Karpanty, C. Crawford, M. Kotschwar & J. Randrianantenaina, 2010. An assessment of carnivore relative abundance and density in the eastern rainforests of Madagascar using remotely-triggered camera traps. Oryx, 44: 219–222.
- Gerber, B. D., 2010. Comparing Density Analyses and Carnivore Ecology in Madagascar's Southeastern Rainforest. Unpublished Masters Thesis, Virginia Tech, Blacksburg, USA. 182 pp.
- Gerber, B. D., S. M. Karpanty & M. J. Kelly, 2012. Evaluating the potential biases in carnivore capture–recapture studies associated with the use of lure and varying density estimation techniques using photographic-sampling data of the Malagasy civet. *Population Ecology*, **54**: 43–54.
- Gilks, W. R., A. Thomas & D. J. Spiegelhalter, 1994. A language and program for complex Bayesian modelling. *Journal of the Royal* Statistical Society, Series D (The Statistician), 43: 169–177.

- Global Tiger Initiative, 2010. Global Tiger Recovery Program. *Tiger Summit 2010*. St. Petersburg, Russia.
- Goetz, R. G., 1981. A photographic system for multiple automatic exposures under field conditions. *Journal of Widlife Management*, 45: 273–276.
- Goldman, H. V. & J. Winther-Hansen, 2003. First photographs of the Zanzibar servaline Genet Genetta servalina archeri and other endemic subspecies on the island of Unguja, Tanzania. Small Carnivore Conservation, 29: 1–4.
- Gomez, H., R. B. Wallace, G. Ayala & R. Tejada, 2005. Dry season activity periods of some Amazonian mammals. Studies on Neotropical Fauna and Environment, 40: 91–95.
- Gompper, M. E., R. W. Kays, J. C. Ray, S. D. Lapoint, D. A. Bogan & J. R. Cryan, 2006. A comparison of noninvasive techniques to survey carnivore communities in Northeastern North America. *Wildlife Society Bulletin*, 34: 1142–1151.
- Grassman Jr., L. I., M. E. Tewes & N. J. Silvy, 2005. From the Field: Armoring the Camtrakker® cameratrap in a tropical Asian forest. *Wildlife Society Bulletin*, **33**: 349–352.
- Griffith, M., 1993. The Javan Rhino of Ujung Kulon: An Investigation of its Population and Ecology through Camera-Trapping. Directorate General of Forest Protection and Nature Conservation and the World Wide Fund for Nature Indonesia Program, Jakarta, Indonesia. 92 pp.
- Griffith, M. & C. P. van Schaik, 1993. The impact of human traffic on the abundance and activity periods of Sumatran rain forest wildlife. *Conservation Biology*, 7: 623–626.
- Griffiths, M. & C. P. van Schaick, 1993. Camera-trapping: A new tool for the study of elusive rain forest animals. *Tropical Biodiversity*, 1: 131–135.
- Guggisberg, C. A. W., 1977. Early Wildlife Photographers. Taplinger, New York, USA. 128 pp.
- Guillera-Arroita, G., M. S. Ridout & B. J. T. Morgan, 2010. Design of occupancy studies with imperfect detection. *Methods in Ecology and Evolution*, 1: 131–139.
- Guisan, A. & N. E. Zimmermann, 2000. Predictive habitat distribution modeling in ecology. *Ecological Modelling*, 135: 147–186.
- Harihar, A., B. Pandav & S. P. Goyal, 2009. Responses of tiger (*Panthera tigris*) and their prey to removal of anthropogenic influences in Rajaji National Park, India. *European Journal of Wildlife Research*, 55: 97–105.
- Hariyadi, A. R. S., A. Priambudi, R. Setiawan, D. Daryan, A. Yayus & H. Purnama, 2011. Estimating the population structure of Javan rhinos (*Rhinoceros sondaicus*) in Ujung Kulon National Park using the mark recapture method based on video and camera trap identification. *Pachyderm*, 49: 90–99.
- Harris, G., R. Thompson, J. L. Childs & J. G. Sanderson, 2010. Automatic storage and analysis of camera trap data. Bulletin of the Ecological Society of America, 91: 352–360.
- Hebeisen, C., J. Fattebert, E. Baubet & C. Fischer, 2008. Estimating wild boar (Sus scrofa) abundance and density using capture resights in Canton of Geneva, Switzerland. European Journal of Wildlife Research, 54: 391–401.
- Hegglin, D., P. Deplazes, F. Bontadina, S. Gloor, J. Romer, U. Muller & U. Breitenmoser, 2004. Baiting red foxes in an urban area: A camera trap study. *Journal of Wildlife Management*, 68: 1010–1017.
- Heilbrun, R. D., N. J. Silvy, M. J. Peterson & M. E. Tewes, 2003. Using automatically triggered cameras to individually identify bobcats. *Wildlife Society Bulletin*, 31: 748–755.

- Henschel, P. & J. Ray, 2003. Leopards in African rainforests: Survey and monitoring techniques. *WCS Global Carnivore Program*. Wildlife Conservation Society, Toronto, Canada. 49 pp.
- Hiby, L., P. Lovell, N. Patil, N. S. Kumar, A. M. Gopalaswamy & K. U. Karanth, 2009. A tiger cannot change its stripes: Using a three-dimensional model to match images of living tigers and tiger skins. *Biology Letters*, 5: 383–386.
- Hines, J. E., 2006. *Program PRESENCE Version 2.4*, Patuxent Widlife Research Center, Laurel, USA.
- Hines, J. E., J. D. Nichols, J. A. Royle, D. I. MacKenzie, A. M. Gopalaswamy, N. S. Kumar & K. U. Karanth, 2010. Tigers on trails: Occupancy modeling for cluster sampling. *Ecological Applications*, 20: 1456–1466.
- Hosmer, D. W. & S. Lemeshow, 1989. *Applied Logistic Regression*. John Wiley & Sons, New York, USA.
- Hutajulu, M. B., Sunarto, S. Klenzendorf, J. Supriatna, A. Budiman & A. Yahya, 2007. Study on the ecological characteristics of clouded leopards in Riau, Sumatra. SSC Cat Specialist Group Conference Proceedings. Oxford University, Oxford, UK.
- Jackson, R. M., J. D. Roe, R. Wangchuk & D. O. Hunter, 2006. Estimating snow leopard population abundance using photography and capture-recapture techniques. *Wildlife Society Bulletin*, 34: 772–781.
- Jennelle, C. S., M. C. Runge & D. I. MacKenzie, 2002. The use of photographic rates to estimate densities of tigers and other cryptic mammals: A comment on misleading conclusions. *Animal Conservation*, **5**: 119–120.
- Karanth, K. K., J. D. Nichols, J. E. Hines, K. U. Karanth & N. L. Christensen, 2009. Patterns and determinants of mammal species occurrence in India. *Journal of Applied Ecology*, 46: 1189–1200.
- Karanth, K. U., 1995. Estimating tiger *Panthera tigris* populations from camera-trap data using capture recapture models. *Biological Conservation*, 71: 333–338.
- Karanth, K. U., R. S. Chundawat, J. D. Nichols & N. S. Kumar., 2004a. Estimation of tiger densities in the tropical dry forests of Panna, Central India, using photographic capture–recapture sampling. *Animal Conservation*, 7:285–290.
- Karanth, K. U., J. D. Nichols & N. S. Kumar., 2011. Estimating tiger abundance from camera trap data: Field surveys and analytical issues. In: A. F. O'Connell, J. D. Nichols & U. K. Karanth (eds.), Camera Traps in Animal Ecology: Methods and Analyses. Springer, New York. Pp. 97–118.
- Karanth, K. U. & J. D. Nichols, 1998. Estimation of tiger densities in India using photographic captures and recaptures. *Ecology*, 79: 2852–2862.
- Karanth, K. U., J. D. Nichols & N. S. Kumar, 2004b. Photographic sampling of elusive mammals in tropical forest. In: W. L. Thompson (ed.), Sampling rare or elusive species: Concepts, designs, and techniques for estimating population parameters.
 Island Press, Washington DC. Pp. 229–247.
- Karanth, K. U., J. D. Nichols, N. S. Kumar & J. E. Hines, 2006. Assessing tiger population dynamics using photographic capture-recapture sampling. *Ecology*, **8**7: 2925–2937.
- Kawanishi, K. & M. Sunquist, 2004. Conservation status of tigers in a primary rainforest of Peninsular Malaysia. *Biological Conservation*, 120: 329–344.
- Kays, R. W. & K. M. Slauson, 2008. Remote cameras. In: Long, R. A., P. MacKay, W. J. Zielinski & J. C. Ray (eds.), *Noninvasive Survey Methods for Carnivores*. Island Press, Washington DC. Pp. 110–140.

- Keating, K. A. & S. Cherry, 2004. Use and interpretation of logistic regression in habitat-selection studies. *Journal of Wildlife Management*, 68: 774–789.
- Kelly, J. M. & E. L. Holub, 2008. Camera trapping of carnivores: Trap success among camera types and across species, and habitat selection by species on Salt Pond Mountain, Giles Country, Virginia. *Northeastern Naturalist*, 15: 249–262.
- Kelly, M., A. Noss, M. Di Bitetti, L. Maffei, R. Arispe, A. Paviolo, C. De Angelo & Y. Di Blanco, 2008. Estimating puma densities from camera trapping across three study sites: Bolivia, Argentina, and Belize. *Journal of Mammalogy*, 89: 408–418.
- Kelly, M. J., 2001. Computer-aided photograph matching in studies using individual identification: An example from Serengeti Cheetahs. *Journal of Mammalogy*, 82: 440–449.
- Kelly, M. J., 2008. Design, evaluate, refine: Camera trap studies for elusive species. *Animal Conservation*, **11**: 182–184.
- Kendall, W. L. & J. D. Nichols, 1995. On the use of secondary capture-recapture samples to estimate temporary emigration and breeding proportions. *Journal of Applied Statistics*, 22: 751–762.
- Kendall, W. L., J. D. Nichols & J. E. Hines. 1997. Estimating temporary emigration using capture-recapture data with Pollock's robust design. *Ecology*, 78: 563–578.
- Kery, M., B. Gardner, T. Stoeckle, D. Weber & J. A. Royle, 2010. Use of spatial capture-recapture modeling and DNA data to estimate densities of elusive animals. *Conservation Biology*, 25: 356–364.
- Kucera, T. E. & H. H. Barrett, 2011. A history of camera trapping. In: O'Connell, A. F., J. D. Nichols & K. U. Karanth (eds.), Camera Traps in Animal Ecology: Methods and Analyses. Springer, New York, USA. Pp. 9–26.
- Krebs, C., 1989. Ecological Methodology. Harper Collins, New York, USA. 624 pp.
- Link, W. A. & J. R. Sauer, 1998. Estimating population change from count data: Application to the North American Breeding Bird Survey. *Ecological Applications*, 8: 258–268.
- Linkie, M., G. Chapron, D. J. Martyr, J. Holden & N. Leader-Williams, 2006. Assessing the viability of tiger subpopulations in a fragmented landscape. *Journal of Applied Ecology*, 43: 576–586.
- Linkie, M., Y. Dinata, A. Nugroho & I. A. Haidir, 2007. Estimating occupancy of a data deficient mammalian species living in tropical rainforests: Sun bears in the Kerinci Seblat region, Sumatra. *Biological Conservation*, **137**: 20–27.
- Linkie, M. & M. S. Ridout, 2011. Assessing tiger–prey interactions in Sumatran rainforests. *Journal of Zoology*, **284**: 224–229.
- Linkie, M., H. T. Wibisono, D. J. Martyr & Sunarto, 2008. Panthera tigris ssp. sumatrae In: IUCN 2013. IUCN Red List of Threatened Species. Version 2013.1. http://www.iucnredlist. org/details/15966/0.
- Lorenzana Pina, G. P., R. A. Castillo Gamez & C. A. Lopez Gonzalez, 2004. Distribution, habitat association, and activity patterns of medium and large-sized mammals of Sonora, Mexico. *Natural Areas Journal*, 24: 354–357.
- Lyra-Jorge, M. C., G. Ciocheti, V. R. Pivello & S. T. Meirelles, 2008. Comparing methods for sampling large- and medium-sized mammals: Camera traps and track plots. *European Journal of Wildlife Research*, 54: 739–744.
- Mace, R. D., S. C. Minta, T. L. Manley & K. E. Aune, 1994. Estimating grizzly bear population size using camera sightings. *Wildlife Society Bulletin*, 22: 74–82.

- MacKenzie, D. I., 2005. What are the issues with presence-absence data for wildlife managers? *Journal of Wildlife Management*, 69: 849–860.
- MacKenzie, D. I., J. D. Nichols, J. A. Royle, K. H. Pollock, L. L. Bailey & J. E. Hines, 2006. Occupancy Estimation and Modelling: Inferring Patterns and Dynamics of Species Occurrence. Elsevier, New York. 344 pp.
- MacKenzie, D. I., J. D. Nichols, N. Sutton, K. Kawanishi & L. L. Bailey, 2005. Improving inferences in population studies of rare species that are detected imperfectly. *Ecology*, 86: 1101–1113.
- MacKenzie, D. I. & J. A. Royle, 2005. Designing occupancy studies: General advice and allocating survey effort. *Journal of Applied Ecology*, **42**: 1105–1114.
- Maffei, L., E. Cuellar & A. Noss, 2004. One thousand jaguars (*Panthera onca*) in Bolivia's Chaco? Camera trapping in the Kaa-Iya National Park. *Journal of Zoology*, **262**: 295–304.
- Maffei, L. & A. J. Noss, 2008. How small is too small? Camera trap survey areas and density estimates for ocelots in the Bolivian Chaco. *Biotropica*, **40**: 71–75.
- Manly, B. F. J., L. L. McDonald, D. L. Thomas, T. L. McDonald & W. P. Erickson, 2002. Resource Selection by Animals: Statistical Design and Analysis for Field Studies. 2nd Edition. Springer Netherlands, Netherlands. 221 pp.
- Marques, T. A., L. Thomas & J. A. Royle, 2011. A hierarchical model for spatial capture-recapture data: Comment. *Ecology*, 92:526–528.
- Martins, Q. & N. Martins, 2006. Leopards of the Cape: Conservation and conservation concerns. *International Journal of Environmental Studies*, **63**: 579–585.
- Martins, S. d. S., J. G. Sanderson & J. d. S. Silva-Junior, 2007.
 Monitoring mammals in the Caxiuana National Forest, Brazil
 First results from the Tropical Ecology, Assessment and Monitoring (TEAM) program. *Biodiversity Conservation*, 16: 857–870.
- Mohd-Azlan, J., 2009. The use of camera traps in Malaysian rainforests. *Journal of Tropical Biology and Conservation*, 5: 81–86.
- Mohamed, A., R. Sollmann, H. Bernard, L. N. Ambu, P. Lagan, S. Mannan, H. Hofer, A. Wilting, 2013. Density and habitat use of the leopard cat (*Prionailurus bengalensis*) in three commercial forest reserves in Sabah, Malaysian Borneo. *Journal* of Mammalogy, 94, 82–89.
- Mohd-Azlan, J. & D. S. K. Sharma, 2003. Camera trapping the Indochinese tiger, *Panthera tigris corbetti*, in a secondary forest in Peninsular Malaysia. *Raffles Bulletin of Zoology*, **51**: 421–427.
- Moruzzi, T. L., T. K. Fuller, R. M. DeGraaf, R. T. Brooks & W. Li, 2002a. Assessing remotely triggered cameras for surveying carnivore distribution. *Wildlife Society Bulletin*, **30**: 380–386.
- Moruzzi, T. L., T. K. Fuller, R. M. DeGraaf, R. T. Brooks & W. Li, 2002b. Assessing remotely triggered cameras for surveying carnivore distribution. *Wildlife Society Bulletin*, **30**: 380–386.
- Moynihan, T., 2010 Fujifilm unveils its second-generation 3D camera. In: Fox, S. (ed.), *PC World*. International Data Group (IDG), Boston, USA.
- Negrões, N., P. Sarmento, J. Cruz, C. Eira, E. Revilla, C. Fonseca, R. Sollmann, N. M. Tôrres, M. M. Furtado, A. T. A. Jácomo & L. Silveira, 2010. Use of camera-trapping to estimate puma density and influencing factors in Central Brazil. *Journal of Wildlife Management*, 74: 1195–1203.
- O'Brien, T. 2011. Abundance, density and relative abundance: A conceptual framework. In: O'Connel, A. F., J. D. Nichols & K.

- U. Karanth (eds.), Camera Traps in Animal Ecology: Methods and Analyses. Springer, New York. Pp. 71–96.
- O'Brien, T. G., M. F. Kinnaird & H. T. Wibisono, 2003. Crouching tigers, hidden prey: Sumatran tiger and prey populations in a tropical forest landscape. *Animal Conservation*, 6: 131–139.
- O'Connell, A. F., J. D. Nichols & K. U. Karanth, 2011a. *Camera Traps in Animal Ecology*. Springer, New York, USA. 280 pp.
- O'Connell, A. F., J. D. Nichols & K. U. Karanth, 2011b. Introduction. In: O'Connel, A. F., J. D. Nichols & K. U. Karanth (eds.), *Camera Traps in Animal Ecology*. Springer, New York, USA. Pp. 1–8.
- O'Brien, T. G., 2008. On the use of automated cameras to estimate species richness for large- and medium-sized rainforest mammals. *Animal Conservation*, 11: 179–181.
- O'Brien, T. G., J. E. M. Baillie, L. Krueger & M. Cuke, 2010. The Wildlife Picture Index: Monitoring top trophic levels. *Animal Conservation*, 13: 335–343.
- O'Brien, T. G. & M. F. Kinnaird, 2008. A picture is worth a thousand words: The application of camera trapping to the study of birds. *Bird Conservation International*, **18**: S144–S162.
- O'Brien, T. G. O, 2011. Abundance, density and relative abundance: A conceptual framework. In: O'Connell, A. F., J. D. Nichols & K. U. Karanth (eds.), *Camera Traps in Animal Ecology: Methods and Analyses*. Springer, New York, USA. Pp. 71–96.
- Oliveira-Santos, L. G. R., M. A. Tortato & M. 1. E. Graipel, 2008. Activity pattern of Atlantic Forest small arboreal mammals as revealed by camera traps. *Journal of Tropical Ecology*, **24**: 563–567.
- Otis, D. L., K. P. Burnham, G. C. White & D. R. Anderson, 1978. Statistical inference from capture data on closed animal populations. *Wildlife Monographs*, 62: 135.
- Pearson, O. P., 1959. A traffic survey of Microtus-Reithrodontomys runways. *Journal of Mammalogy*, 40: 169–180.
- Pettorelli, N., A. L. Lobora, M. J. Msuha, C. Foley & S. M. Durant, 2010. Carnivore biodiversity in Tanzania: Revealing the distribution patterns of secretive mammals using camera traps. *Animal Conservation*, 13: 131–139.
- Pollock, K. H., J. D. Nichols, C. Brownie & J. E. Hines, 1990. Statistical inference for capture-recapture experiments. Wildlife Monographs, 107: 1–97.
- Pollock, K. H., J. D. Nichols, T. R. Simons, G. L. Farnsworth, L. L. Bailey & J. R. Sauer, 2002. Large scale wildlife monitoring studies: Statistical methods for design and analysis. *Environmetrics*, 13: 105–119.
- Rayan, D. M. & S. W. Mohamad, 2009. The importance of selectively logged forests for tiger *Panthera tigris* conservation: A population density estimate in Peninsular Malaysia. *Oryx*, 43: 48–51.
- Rexstad, E. & K. Burnham, 1992. User's Guide for Interactive Program CAPTURE. Colorado State University, Fort Collins, USA. 30 pp.
- Ridout, M. S. & M. Linkie, 2009. Estimating overlap of daily activity patterns from camera trap data. *Journal of Agricultural*, *Biological, and Environmental Statistics*, 14: 322–337.
- Rovero, F., M. Tobler & J. Sanderson, 2010. Camera trapping for inventorying terrestrial vertebrates. In: Jutta Eymann, J. D., Christoph Häuser, Juan Carlos Monje, Yves Samyn & Didier Van den Spiegel (eds.), Manual On Field Recording Techniques and Protocols for All Taxa Biodiversity Inventories. Belgium Focal Point to the GTI, Brussels, Belgium. Pp. 29.

- Rowcliffe, J. M., J. Field, S. T. Turvey & C. Carbone, 2008. Estimating animal density using camera traps without the need for individual recognition. *Journal of Applied Ecology*, 45: 1228–1236.
- Royle, J. A. & J. D. Nichols, 2003. Estimating abundance from repeated presence-absence data or point counts. *Ecology*, 84: 777–790.
- Royle, J. A., J. D. Nichols, K. U. Karanth, and A. M. Gopalaswamy, 2009. A hierarchical model for estimating density in camera-trap studies. Journal of Applied Ecology 46:118–127.
- Royle, J. A. & R. M. Dorazio, 2008. *Hierarchical Modeling and Inference in Ecology*. Academic Press, London, UK. 464 pp.
- Royle, J. A. & B. Gardner, 2011. Hierarchical spatial capture-recapture models for estimating density from trapping arrays. In: O'Connell, A. F., J. D. Nichols & K. U. Karanth (eds), *Camera Traps in Animal Ecology: Methods and Analyses*. Springer, New York, USA. Pp. 163–190
- Royle, J. A. & K. V. Young, 2008. A hierarchical model for spatial capture-recapture data. *Ecology*, **89**: 2281–2289.
- Sanderson, J. G., 2009. How the fishing cat came to occur in Sumatra. *Cat News*, **50**: 6–9.
- Sanderson, J. G. & M. Trolle. 2005. Monitoring elusive mammals: Unattended cameras reveal secrets of some of the world's wildest places. *American Scientist*, 93: 148–155.
- Selmi, S. & T. Boulinier, 2003. Does time of season influence bird species number determined from point-count data? A capture-recapture approach. *Journal of Field Ornithology*, 74: 349–356.
- Sequin, E. S., P. F. Brussard, M. M. Jaeger & R. H. Barrett, 2003. Wariness of coyotes to camera traps relative to social status and territory boundaries. *Canadian Journal of Zoology*, **81**: 2015–2025.
- Sharma, R. K., Y. Jhala, Q. Qureshi, J. Vattakaven, R. Gopal & K. Nayak, 2010. Evaluating capture–recapture population and density estimation of tigers in a population with known parameters. *Animal Conservation*, **13**: 94–103.
- Silveira, L., A. T. A. Jacomo & J. A. F. Diniz-Filho, 2003. Camera trap, line transect census and track surveys: A comparative evaluation. *Biological Conservation*, **114**: 351–355.
- Silver, C. S., L. E. T. Ostro, L. K. Marsh, L. Maffei, A. J. Noss, M. J. Kelly, R. B. Wallace, H. Gómez & G. Ayala, 2004. The use of camera traps for estimating jaguar *Panthera onca* abundance and density using capture/recapture analysis. *Oryx*, **38**: 148–154.
- Silver, S., 2004. Assessing Jaguar Abundance Using Remotely Triggered Cameras. Widlife Conservation Society, New York, USA. 25 pp.
- Simpson, E. H. 1949. Measurement of diversity. Nature, 163: 688.
- Singh, P., A. M. Gopalaswamy, A. J. Royle, N. S. Kumar, K. U. Karanth, S. Mukherjee, Vatsaraj & D. Bharadwaj, 2010. Package 'SPACECAP': A program to estimate animal abundance and density using spatially-explicit capture-recapture. *Methods in Ecology and Evolution*, 3: 1067–1072.
- Soehartono, T., H. T. Wibisono, Sunarto, D. Martyr, H. D. Susilo, T. Maddox & D. Priatna, 2007. Strategi dan rencana aksi konservasi harimau Sumatera (*Panthera tigris sumatrae*) 2007–2017 In: D. Kehutanan (ed.), *Peraturan Menteri Kehutanan Nomor: P.42/Menhut-Ii/2007*. Departemen Kehutanan, Jakarta, Indonesia.
- Soisalo, M. K. & S. M. C. Cavalcanti, 2006. Estimating the density of a jaguar population in the Brazilian Pantanal using cameratraps and capture-recapture sampling in combination with GPS radio-telemetry. *Biological Conservation*, **129**: 487–496.

- Sollmann, R., M. M. Furtado, B. Gardner, H. Hofer, A. T. A. Jácomo, N. M. Tôrres & L. Silveira, 2011. Improving density estimates for elusive carnivores: Accounting for sex-specific detection and movements using spatial capture–recapture models for jaguars in central Brazil. *Biological Conservation*, 144: 1017–1024.
- Sollmann, R., M. M. Furtado, H. Hofer, A. T. Jácomo, N. M. Tôrres & L. Silveira, 2012. Using occupancy models to investigate space partitioning between two sympatric large predators, the jaguar and puma in central Brazil. *Mammalian Biology-Zeitschrift für Säugetierkunde*, 77: 41–46.
- Sunarto, 2011. Ecology and Restoration of Sumatran Tigers in Forest and Plantation Landscapes. Unpublished PhD Thesis, Virginia Tech, Blacksburg, USA. 261 pp.
- Sunarto, M. Bismark, W. Sukmantoro, Boeadi & B. O. Manullang, 2004. Keanekaragaman mamalia dan burung di kawasan Taman Nasional Batang Gadis, Sumatera Utara. Conservation International, Indonesia.
- Sunarto, M. J. Kelly, S. Klenzendorf, M. R. Vaughan, Zulfahmi, M. B. Hutajulu & K. Parakkasi, 2013. Threatened predators on the equator: Multi-point abundance estimates of the tiger *Panthera tigris* in central Sumatra. *Oryx*, 47: 211–220.
- Sundaresan, S. R., C. Riginos & E. S. Abelson, 2011. Management and analysis of camera trap data: Alternative approaches (response to Harris et al. 2010). Bulletin of the Ecological Society of America, 92: 188–195.
- Swann, D. E., K. Kawanishi & J. Palmer, 2011. Evaluating types and features of camera traps in ecological studies: A guide for researchers. In: O'Connell, A. F., J. D. Nichols & K. U. Karanth, (eds.), Camera Traps in Animal Ecology: Methods and Analyses. Springer, New York. Pp. 27–43
- Tilson, R., H. Defu, J. Muntifering & P. J. Nyhus, 2004. Dramatic decline of wild South China tigers *Panthera tigris amoyensis*: Field survey of priority tiger reserves. *Oryx*, **38**: 40–47.
- Tobler, M., 2010. *Camera Base*. San Diego Zoo Institute for Conservation Research, San Diego, USA.
- Tobler, M. W., S. E. Carrillo-Percastegui, R. L. Pitman, R. Mares & G. Powell, 2008. An evaluation of camera traps for inventorying large- and medium-sized terrestrial rainforest mammals. *Animal Conservation*, 11: 169–178.
- Tobler, M. W., S. E. Carrillo-Percastegui & G. Powell, 2009. Habitat use, activity patterns and use of mineral licks by five species of ungulate in south-eastern Peru. *Journal of Tropical Ecology*, 25: 261–270.
- Tracey, J. P., P. J. S. Fleming & G. J. Melville, 2005. Does variable probability of detection compromise the use of indices in aerial surveys of medium-sized mammals? *Wildlife Research*, 32: 245–252.

- Tredick, C. A. & M. R. Vaughan, 2009. DNA-based population demographics of black bears in coastal North Carolina and Virginia. *Journal of Wildlife Management*, **73**: 1031–1039.
- Trolle, M. & M. Kery, 2003. Estimation of ocelot density in the pantanal using capture-recapture analysis of camera-trapping data. *Journal of Mammalogy*, **84**: 607–614.
- Trolle, M. & M. Kery, 2005. Camera-trap study of ocelot and other secretive mammals in the northern Pantanal. *Mammalia*, **69**: 409–416.
- Trolle, M., A. J. Noss, E. D. S. Lima & J. C. Dalponte, 2007. Camera-trap studies of maned wolf density in the Cerrado and the Pantanal of Brazil. *Biodiversity and Conservation*, 16: 1197–1204.
- van Schaik, C. P. & M. Griffiths, 1996. Activity periods of Indonesian rain forest mammals. *Biotropica*, **28**: 105–112.
- Wallace, R. B., H. Gomez, G. Ayala & F. Espinoza, 2003. Camera trapping for jaguar (*Panthera onca*) in the Tuichi Valley, Bolivia. *Journal of Neotropical Mammal*, 10: 133–139.
- Weckel, M., W. Giuliano & S. Silver, 2006. Jaguar (*Panthera onca*) feeding ecology: Distribution of predator and prey through time and space. *Journal of Zoology*, **270**: 25–30.
- Wegge, P., C. P. Pokheral & S. R. Jnawali, 2004. Effects of trapping effort and trap shyness on estimates of tiger abundance from camera trap studies. *Animal Conservation*, 7: 251–256.
- White, G. C., 2009. *Program Mark*. Colorado State University, Fort Collin, USA.
- Wibisono, H. T. & J. McCarthy, 2010. Melanistic marbled cat from Bukit Barisan Selatan National Park, Sumatra, Indonesia. *Cat News*, 52: 9–10.
- Williams, B. K., J. D. Nichols & M. J. Conroy, 2002. *Analysis and Management of Animal Populations: Modelling, Estimation, and Decision Making*. Academic Press, New York, USA. 817 pp.
- Wilson, K. R. & D. R. Anderson, 1985. Evaluation of two density estimators of small mammal population size. *Journal of Mammalogy*, **66**: 13–21.
- Wilting, A., A. Mohamed, L. N. Ambu, P. Lagan, S. Mannan, H. Hofer & R. Sollmann, 2012. Density of the vulnerable Sunda clouded leopard *Neofelis diardi* in two commercial forest reserves in Sabah, Malaysian Borneo. *Oryx*, **46**: 423–426.
- Wolf, K. N., F. Elvinger & J. L. Pilcicki, 2003. Infrared-triggered photography and tracking plates to monitor oral rabies vaccine bait contact by raccoons in culverts. *Wildlife Society Bulletin*, 31: 387–391.
- Wong, S. T., C. Servheen, L. Ambu & A. Norhayati, 2005. Impacts of fruit production cycles on Malayan sun bears and bearded pigs in lowland tropical forest of Sabah, Malaysian Borneo. *Journal of Tropical Ecology*, **21**: 627–639.

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APPENDIX 1: EXAMPLE OF LIST OF CAMERA TRAPPING EQUIPMENT

- Map
- Compass
- GPS unit
- Extra AA batteries for GPS unit
- Radio and/or cell satellite phone
- Data sheet
- Keys for padlocks (if cameras are locked)
- Laminated sheet (or dry erase board) or placard, for writing date, camera, and station number
- Permanent marker
- Ball point pen or pencil
- Dry erase pen
- Rag to wipe off dry erase pen
- Extra bungee cords or nylon webbing
- Extra ziplock baggies to put film or cards in from cameras
- Extra sign (camera trapping "project sign" if needed)
- Alcohol prep pads for cleaning debris from camera O-rings.
- Umbrella –if raining
- Tape measure (for taking trail measurements)
- Machete or other vegetation cutting device (for clearing vegetation around camera)
- Pocket-size multi-tool (always useful)
- Weapons to protect yourself from dangerous animals (mace, gun, spray etc.).
- Spare camera trap for malfunctions
- Spare batteries (model specific)
- Spare memory cards/film rolls (model specific)

APPENDIX 2: EXAMPLE OF A "SET-UP" CAMERA DATA SHEET FOR THE INITIAL DEPLOYMENT OF CAMERA TRAPS IN THE FIELD

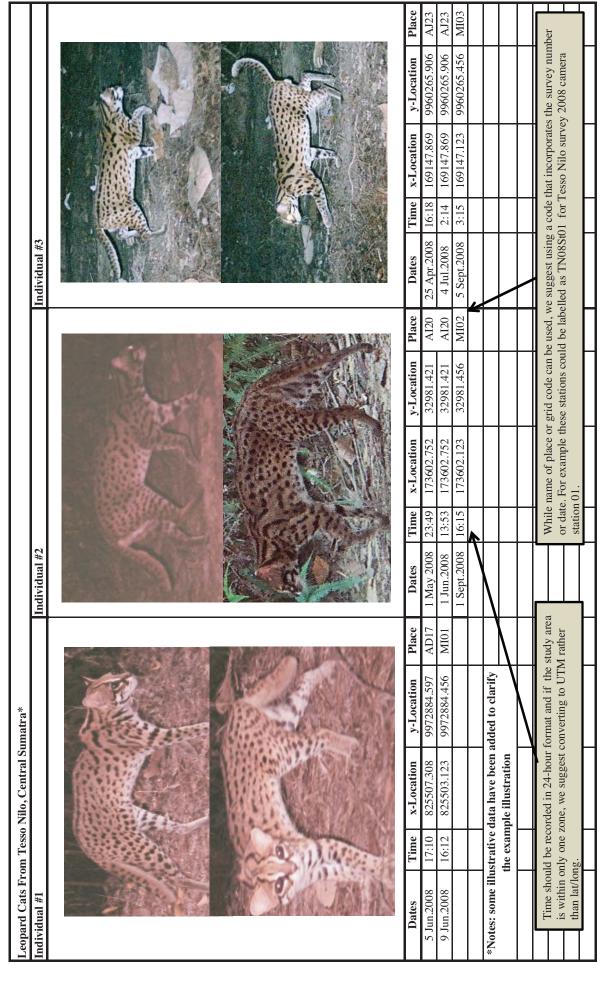
SITE:	resso N	SITE: Tesso Nilo Forest Complex (TNFC)	omplex (TN	FC)		Road (R), Trail (T)		Distance				
Station	Camera #s	Physical Location	Date (D/M/Y)	GPS Location Easting (UTM X)	GPS Location Northing (UTM Y)	New Trail (NT), Game Trail (G)	Width of Road or Trail (m)	Camera to Canopy Middle of Cover (%) Land Road or at Station Use Trail (m) ***	Canopy Cover (%) I at Station 1	· · · ·	Habitat Type ****	Notes
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TW11St02	, MT01	Naniak mara	23 Mar 2011	825503 123	957 7887 700	۲		1.9	Vo	ρδ	A.S.	
701611111	MT08	ınanıjan utara	23 Mai 2011	0223003.123	064:4007166	Þ	1	2.0	2	V.		
TN11St03	MT12	-Naniak selatan	23 Mar.2011	169147.123	9960265.456	×	3.5	4.7	70	PA	PF	
	MT14	,		*	K	K		5.0	•	V	K	
	4											
This exar	This example uses two cameras		Unless the study	Unless the study site encompasses several zones, it	t	Trail type, width, and canopy cover have been shown to be	th, and cano	py cover hav	re been sho	wn to be		It is a good idea to collect categorical
per statio for Moul	per station. In this case MT for Moultrie brand camera.	stands	may be beuer to lat/long. Since U	may be better to use 0.11M coordinates rather man lat/long. Since UTMs are in meters, it is easy to tel distances away from cameras or distances between		productions of uncontained among factors when a service of one of the production of	ct this data.	In addition, or make sure the	distance fro	of put you		data about each location. These codes can be very specific to your study.
			cameras stations.			camera so far away. This is to ensure that the nightime flash or	way. This is	to ensure th	at the nigh	time flash	or	
		·			ha	ninated will at least feach the target area. Camera inancs an have different flash/infra ranges.	Tash/infra ra	inges.	ca. Callicia	IIIancs all		/
								П				7
** Canop *** Land *** Hahi	y cover: 0 = use: PA pr	= 0-10%, 10 = 10-2 rotected area, OP	20%, 20 = 20-30 oil palm plantat	** Canopy cover: 0 = 0-10%, 10 = 10-20%, 20 = 20-30%, 30 = 30-40%, 40 = 40-50%, 50 = 50-60%, 60 = 60-70%, 70 = 70-80%, 80 = 80-90%, 90 = 90-100%. *** Land use: PA protected area, OP oil palm plantation, AC Accacia, R roads, BA built up area. *** Habitat DE mimory forcet SE coondary forcet SE coo	0 = 40-50%, $50 = 50-60$ roads, BA built up area.)-60%, 60 = 0 orea.	60–70%, 70	0 = 70 - 80%,	,80 = 80–9i	0%,90=	90-100%	6.
IIan	114 . 1 I pi I	many forest, or se	condary rorest,	DO Dusmanu, Gregia	issianu, r.s. n.esii v	rater swamp	, MI IIVCI III	c, i i piant				

APPENDIX 3: EXAMPLE OF A CAMERA CHECKING DATA SHEET USED WHEN MONITORING CAMERAS FOR PROPER FUNCTIONING IN THE FIELD

Site: Tesso Nilo Forest Complex	Forest Compl	ex																		
Survey Name: TNSyst2011	NSyst2011					Put a	heck ma	rk for 1	things th	Put a check mark for things that you have checked and a dash if nothing needed	ave che	cked an	d a das	h if noth	ning nee	ded				
Station Code or Station #	Camera Type & Number MT = Moultrie RE = Reconyx DC = DerCam BEC = Buckeye	Names or Initials of Camera checkers	Today's Date (d/m/yy)	Trigger with Station #, Camera #, and Date on Display Card	# Pics Taken	Open Camera. Press Off Button for DCs, BEs or MTs, DON'T TURN OFF BEC DIGITALS Bettern Lovel & for Divisels on # of Green	Baitery Level % for Digitals or # of Green Blinks for DCs (9-volts)	Change Batteries? Yes (Y) NO (N) Which Batteries Changed? AAs, 9-Volts,	Cs, Ds, 6 Volts Catd or Film Swapped Out, or Images	Downloaded to Card? Yes (Y) or No (N) Digitals on Still Picture Mode (S) or Video	Mode (V) Image Quality? High (H), Med (M), Low	(L) Event Delay in Minutes	# Pictures per Event	Check Date/Time Stamp on Camera- is it Correct?	Clean O-Rings (Camera Seal) with Cloth	Clean Lens Cover, Flash Cover and Sensor Cover	Set, Lock, and Reposition	Make Sure Camera is On (AUTO for MTs or Switch for REs)	Trigger with Station #, Camera #, and Date on Display card	Notes - include anything out of the ordinary, damage to cameras by animals, suspected malfunctions, physical location if you change a camera location etc.
, 0.00 km	MT04	,		ä	69			z			S	4	ю	æ	ņ	ij	ä	ä	;	Very dirty from water splash up - cleaned lenses, o-rings well
INIIStol	MT15	SS, MJK, KS	13 Apr.2011	ü	78	ü	18%	Z		Υ	S	L 1	3	ü	ü	ü	ü	ü	ü n	Camera out of position slightly and with some claw marks. Re-arranged and repositioned to fix.
COSTINA	MT01	SG MIK SS	13 Amr 2011		3	ü	75%	Z		Y s	S	M 1	3	ü	ü	ü	ü	ü	ü	Camera did not trigger. Battery read good. Replaced with camera MT25
701011	MT08	55, MJK, K5	1102.145.C1	ņ	112	ü 6	95%	Z		Y s	S	Н	3	ü	ü	ü	ü	ü	ü	
TW115403	MT12	30 AIM 33	13 422 2011	ņ	27	ü	. 72%	Y	Ds	γ	S	M 0.5	3	ü	ü	ü	ü	ü	ü	Changed Ds, then camera read 99% ▲
INITISTOS	MT14	95, MUK, K5	13 Apr.2011	ü	21	ü	80%	z	R	Y				ü	ü	ű	ü	ü	ij	
N N	researchers	Noting researchers present is helpful to				\nearrow		$\downarrow \downarrow$												
addr. Trigg reads Cam tregg	roung researches present is rep- address later questions that might is Trigger camera with a placard that reads at minimum: Station Numbe Camera Number and Date. Separat treggering for each of the 2 camers	rooning toscarcius process is imported address later questions that might arrise. Trigger camera with a placard that reads a minimum: Station Number, Camera Number and Date. Separate treggering for each of the 2 cameras.	3 93	Havin speci forge main numb whett image	Having a check she specific order preve forgetting key informaintenance proced number of photogra whether memory as image quality, etc.	Having a check sheet to follow in a specific order prevents researchers from forgetting key information or maintenance procedure such as noting number of photographs, batterly levels, whether memory cards were changed, image quality, etc.	ow in a urchers fr r r as notin; ery levels changed	oom se se s. '.'		Doubl camer malfur betwee trigger stamp	Double checking all the settings at examera check is important because malfunctions can cause the time between events, # photos taken per trigger, and especially date and time stamp to become corrupted or incorr	ng all the is important caus s, # phope pecially ne corru	ne settin tant bec e the tin tos take date an	Double checking all the settings at each camera check is important because malfunctions can cause the time between events, # photos taken per trigger, and especially date and time stamp to become corrupted or incorrect.	- H	Withc specif flash c easily image efficie	Without a note to specifically check flash or sensor, di easily go unnotice image quality or tefficiency will be efficiency will be compromised.	Without a note to specifically check the lense, specifically check the lense, flash or sensor, dirt can easily go unnoticed and image quality or trigger efficiency will be serously commonised.	lense, n id id yr usly	Re-triggering cameras with the placard (Station#, Camera #, and Date) is particulary important when you have changed the memory card. This will alleviate the need to keep track of which memory card is which since a photographic record is taken. Notes on specific camera issues can be very helpful.
	$\overline{\ \ }$				\dashv	\dashv	-	\dashv	\dashv	H	H	Н	H	Ц	\prod				П	

APPENDIX 4: EXAMPLE OF INDIVIDUAL IDENTIFICATION FOR LEOPARD CATS "CAPTURED" AT REMOTE CAMERA STATIONS

Using 2 cameras per stations allows photographs to be obtained from both the right and left sides of the animal. Printing out such reference sheets makes for easier identification as new photographs come in from the field. Additionally it is easy to build capture histories for each individual from this reference sheet.



APPENDIX 5: EXAMPLE OF DATA ENTRY SPREAD SHEET FOR RAW PHOTO DATA WITH TWO CAMERAS PER STATION

Vehicle/Foot It is good to note the camera numbers and especially or group of photos. In this example, if two cameras fro the second camera. BEC, MT, and RE refers to the image number to later relocate a specific photo camera while all images after the semi-colon came are noted, then both cameras fired. Whereas if one camera is noted, only 1 of the 2 camera fired. All images before the semi-colon came from the first vehicle Buckeye, Moultrie, and Reconyx brand cameras foot foot foot foot foot foot foot Human Type Researchers Researchers Researcher Researcher Jnknown Unknown We suggest entering all data on all species including non-target species and humans as this information can be important in predicting target species presence or abundance **Fourist** Hunter doe and fawn change card hunting dog Bear moved change card Notes Buck cam MT215;RE07 MT215;RE07 BEC17;RX01 BEC17;RX01 BEC17;RX01 BEC17;RX01 MT215;RE07 MT215;RE07 MT215;RE07 MT215;RE07 BEC17;RX01 MT215;RE07 BEC17;RX0] BEC17;RX0] Cam #(s) MT215 MT215 MT215 BEC17 MT215 RX01 RE07 RE07 **RE07 RE07** RE07 **RE07** captures. Most camera studies use 30 or 60 mins as the standard, albeit somewhat arbitrary, cutmore than one event in the photo such as when 2 deer are photographed in 1 picture (4th record off for considering a capture of a new event. Each row denotes an event, however there can be 79-84,1-21; 19-30,1-18 total numbers of photos sifted through to obtain the data. Once in this type of spreadsheet, it is 22-30,55-66;16-27,1-9 above). The total number of photos can be added together from both cameras to keep track of relatively simple to use Pivot Table in Excel to sort the total numbers of events and photos by 634-641;145-192,1-15 34-39; 28-33, 38-39 647-655:25-40 Perhaps the trickiest part is determining the independent "events" or independent animal 632;133-135 633;136-141 642-643;16 28-33; 22-27 16-21;4-6 25; 19-20 121-126 646;22–24 127-129 142-144 1-12;1-210 - 1213-15 69-19 22-24 25-27 10 - 1210 - 1116 - 17545 22 13:44 10:30 10:42 18:38 8:45 17:36 12:55 14:02 11:17 13:29 13:53 19:07 11:16 14:25 1:42 9:29 3:28 4:55 8:32 19:21 9:05 1:45 8:00 9:40 6:28 Date (M/D/Y) 21 Aug.2010 25 Aug.2010 11 Mar.2010 12 Aug.2010 28 Aug.2010 29 Aug.2010 31 Aug.2010 10 Sep.2010 11 Jan.2010 11 Jan.2010 11 Mar.2010 11 Mar.2010 11 Mar.2010 11 Jun.2010 11 Jun.2010 15 Aug.2010 16 Aug.2010 18 Aug.2010 25 Aug.2010 29 Aug.2010 30 Aug.2010 11 Feb.2010 11 Jul.2010 1 Sep.2010 5 Sep.2010 9 Sep.2010 9 Sep.2010 9 Sep.2010 **Photos** 70 33 42 28 4 21 9 m 3 # Animals in Photo animal or camera station. 7MLBS01 7MLBS02 7MLBS02 7MLBS02 'MLBS02 7MLBS02 7MLBS02 7MLBS02 'MLBS02 7MLBS02 7MLBS02 7MLBS02 7MLBS02 7MLBS02 7MLBS02 **7MLBS01** 7MLBS01 7MLBS01 'MLBS02 'MLBS02 7MLBS02 7MLBS02 7MLBS01 7MLBS01 7MLBS01 7MLBS01 7MLBS01 7MLBS01 Odocoileus virginianus Canis lupus familiaris Sciurus carolinensis example form, the 7MLBS01 and 7MLBS02 are the stations 01 and 02 of Ursus americanus Ursus americanus Ursus americanus **Ursus** americanus **Jrsus** americanus Scientific Name this survey. The 7 in front of MLBS Tamias stratus Homo sapiens refers to the fact that this is the 7th Procyon lotor Procyon lotor Procyon lotor followed by a station code. In this Use common and scientific name, survey at the same site. Eastern Chipmunk White-tailed Deer White-tailed Deer White-tailed Deer Vhite-tailed Deer White-tailed Deer White-tailed Deer White-tailed deer White-tailed deer Common Name iray Squirrel Black Bear lack Bear lack Bear lack Bear Black Bear nknown Raccoon accoon accoon Human Human Human **[uman** Iuman Iuman Human luman

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APPENDIX 6: BRIEF GUIDE TO STUDY DESIGN AND DATA ANALYSIS FOR COMMON PURPOSES OF CAMERA TRAPPING

This brief guide will provide basic assistance in designing a camera trapping study and picking adequate analytical techniques depending on what aspect of ecology researchers are trying to investigate. It is by no means an exhaustive list of questions one might ask when using camera traps, or approaches one might adopt for data analysis. Neither is this intended as a manual for camera trap study design and data analysis. Rather, our aim was to cover the more frequently used approaches, touch upon some basic issues a researcher has to consider when designing a study for a specific approach, and provide some literature as a starting point for further reading about the topic. Adequately planning a study is extremely important and this brief guide is intended to get one started.

STARTING POINT: SINGLE SPECIES (1) or MULTI SPECIES (2)

1. SINGLE SPECIES FOCUS

Question: What aspect of research are you interested in?

1.1 Presence – Question: Is my focal species present in the study area?

Option: Use method by Tilson et al. (2004) to estimate minimum effort to determine absence of your target species with more reliability. No particular setup requirements except to increase the probability of detecting the target animal.

1.2 Distribution/habitat use/occupancy – Question: How is my target species distributed in space? Which factors influence the occurrence of my target species?

Individuals of your species can be identified – go to 1.2.1

Otherwise go to 1.2.2

1.3 Abundance/density - Question: How abundant is my target species?

Individuals of your species can be identified - go to 1.3.1

Otherwise go to 1.3.2

1.4 Activity pattern – Question: What time of the day is my target species active/inactive?

Option 1: Percent pictures per time interval (e.g., Cheyne & Macdonald, 2011).

Option 2: Kernel analysis for circular data (Fisher, 1993; Linkie & Ridout, 2011)

No particular setup requirements for either option.

1.5 Population dynamics – Question: How does my study population change over time; what are the demographic rates?

Go to 1.3.1 – capture-recapture modeling; for formal extension of the closed population model of abundance/density to an open population model of population dynamics, see, for example, Pollock et al. (1990) and Karanth et al. (2006).

1.6 Occupancy dynamics – Question: How do patterns of occupancy change over time; what are the rates of local extinction and colonisation?

Go to 1.2.2 – occupancy modeling; for formal extension of the single-season model to a multiple-season model, see MacKenzie et al. (2006), Chapter 7.

1.2.1 Spatial distribution of an individually identifiable species

Option 1: If you have enough data and explanatory variables are available for the entire study site (not just the camera trap point locations) use spatial capture-recapture models and make density a function of your habitat variable. For details, see 1.3.1, Option 2.

All methods under 1.2.2 are also applicable.

1.2.2 Spatial distribution of species (no individual ID)

Option 1: Occupancy models (MacKenzie et al., 2006). Sample units need to be spatially independent, need to cover all relevant environmental conditions, and refer to areas, NOT points.

Option 2: Regression on the number of photographs (log-linear, e.g., Foster et al., 2010) or detection/non-detection (logistic, e.g., Guisan & Zimmermann, 2000) at each site. Sample units need to be spatially independent, need to cover all relevant environmental conditions. However, regressions do not account for imperfect detection, and we suggest using occupancy models.

Data requirements for both options: A fair number of sampling units; explanatory variables for all sampling units.

1.3.1 Abundance of individually distinguishable species

Option 1: Non-spatial capture-recapture (CR) models (e.g., Karanth & Nichols, 1998). Camera trap array should be several times an average home range (Maffei & Noss, 2008); must not contain holes large enough to contain an entire home range; produces abundance estimates, density must be estimated using an ad hoc approach to estimating animal movement.

Data requirements: Several individuals, several recaptures.

Option 2: Spatial capture-recapture (SCR) models (e.g., Royle et al., 2009, Efford, 2011). Camera trap array should cover the extent of animal movement (but not necessarily several times, Marques et al., 2011); can contain some 'holes' but overall spacing should be smaller than animal movement.

Data requirements: Several individuals, several spatially spread out recaptures, potentially individual and spatial explanatory variables.

1.3.2 Abundance of non-distinguishable species

Option 1: Gas model (Rowcliffe et al., 2008). A completely random study setup is required (so think about if this is feasible both in terms of logistics and in terms of the amount of data this will render) and animal movement speed needs to be known or estimated (telemetry data, video traps).

Option 2: Royle-Nichols model (Royle & Nichols, 2003). As this is a type of occupancy model, see 1.2.1 for setup and data requirements. This model will render sampling site specific estimates of abundance, which under many circumstances cannot easily be translated into a study area wide abundance estimate.

Observation: Relative Abundance Indices (RAIs) based on photographic capture rates are often calculated in this situation. However, these can exhibit complex bias. Instead, we suggest considering the use of measures other than abundance or other methodologies.

2 MULTIPLE SPECIES FOCUS

Question: What aspect of research are you interested in?

2.1 Species inventory/richness - Question: What is the composition of the mammal assemblage at my study site? How rich is the mammal assemblage?

Option 1: Make a list of detected species; sample study area with a balanced design (no particular species targeting, although you can target certain focal groups such as terrestrial carnivores) and across different environmental conditions to increase the chance for different species being detected; ideally, complement list with other methodologies (spotlighting); remember that failure to detect is no proof of absence (see also 1.1).

Option 2: Estimate the number of species in the study area accounting for the fact that you likely missed some, i.e., with species accumulation curves (for a review see Colwell & Coddington, 1994) or capture-recapture approaches (Boulinier et al., 1998). Option 3: Estimate species diversity; typical measures are Simpson's diversity index (Simpson, 1949) and the Shannon's diversity index (Krebs, 1989); note that these require some measure of relative abundance and are therefore most likely not suitable for camera trapping data, unless abundance can be determined with sound analytical methods (CR or SCR models, calibrated indices).

2.2 Spatial relationship between species - Question: Do species co-occur or avoid each other spatially?

Option 1: Multi-species occupancy models (e.g., Sunarto, 2011); for setup and data requirements see 1.2.1; see MacKenzie et al. (2006) Chapter 8 and 9 for the formal extension of single species to multi species and community-level occupancy models. Option 2: Regression analysis where data from one species is explanatory variable for the other species (Davis et al., 2010); remember that regressions do not account for imperfect detection or differences in detection between species.

2.3 Temporal relationship between species – Question: How similar are the activity patterns of species?

Option: Generate activity patterns as under 1.4 for species of interest and compare overlap of distributions (Ridout & Linkie, 2009; Linkie & Ridout, 2011)