Evaluating jaguar densities with camera traps

Laguna del Tigre National Park, Maya Biosphere Reserve, Guatemala.
Photo by Rony Garcia

This document is intended to serve as an update to Scott Silver's (2004) manual titled *Assessing jaguar abundance using remotely triggered cameras. Wildlife Conservation, Society*.

It summarizes knowledge gained to date, and presents guidance using the new generation of spatially explicit capture-recapture models, covering the steps from design, through execution and analysis, with the intent of being a helpful reference for a next generation of jaguar population studies.

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INTRODUCTION

Camera traps have been used by biologists for over 100 years. They have proven to be a useful tool, complementing other methods for determining species richness and diversity. They provide a non-invasive method for detecting rare, shy and cryptic species, as well as for identifying species that cannot easily be distinguished from tracks or other sign. Camera traps can also be used to monitor wildlife use of key resources such as salt licks, ponds, and fruiting trees. When armed to operate 24 hours a day, they provide important information on habitat use, behavior and activity patterns. But perhaps the most novel application of camera traps has been to generate information on abundance and population density, in particular applying capture-recapture analytical methods (Cutler & Swann 1999, O'Connell et al. 2011).

This document is designed as an introduction to conducting terrestrial mammal abundance surveys using camera traps with the primary focus being jaguar population estimates. The guidance within is based upon established procedures for mark and recapture analyses of closed populations, using cameras in place of traps, and the natural markings of the target species to recognize "recaptures" in photographs. With the date stamped on the photographs, researchers can measure days or blocks of days as discrete sampling events.

Our colleagues working on Asian tigers *Panthera tigris* pioneered many of the methods discussed here (Karanth 1995, Karanth and Nichols 1998, 2002, Karanth et al. 2004, Simcharoen et al. 2007, Royle et al. 2009a, 2009b, Karanth et al. 2011a, Gopalaswamy et al. 2012). This methodology has been used for many more tiger studies (O'Brien et al. 2003, Kawanishi & Sunquist 2004, Wegge et al. 2004, Johnson et al. 2006, Harihar et al. 2009, Lynam et al. 2009, Wang & Macdonald 2009, Sharma et al. 2010). The methodology has subsequently been applied to estimate abundance of other species whose markings permit individual identifications (Box 1):

Box 1: Abundance estimates by species

Researchers have used individual identification from camera trap photos and capture-recapture methods to estimate abundance for the following species (see Appendix 1 for tips on identifying individuals of some species):

- leopards *Panthera pardus* (Henschel & Ray 2003, Ngoprasert et al. 2007, Balme et al. 2009a, Wang & Macdonald 2009, Chapman & Balme 2010)
- snow leopards *Panthera uncia* (Jackson et al. 2006, McCarthy et al. 2008, Janečka et al. 2011)
- pumas *Puma concolor* (Kelly et al. 2008, Paviolo et al. 2009, Mazzolli 2010, Negrões et al. 2010, Soria-Díaz et al. 2010)
- ocelots *Leopardus pardalis* (Trolle and Kéry 2003, 2005, Maffei et al. 2005, di Bitetti et al. 2006, 2008, Dillon and Kelly 2007, 2008, Kolowski & Alonso 2010, Díaz-Pulido & Payán Garrido 2011)
- Geoffroy's cats *Leopardus geoffroyi* (Cuéllar et al. 2006, Caruso et al. 2012)
- pampas cats *Leopardus colocolo* (Gardner et al. 2010, Reppucci et al. 2011, Caruso et al. 2012)
- bobcats *Lynx rufus* (Heilbrun et al. 2006, Mendoza et al. 2011)
- cheetahs *Acinonyx jubatus* (Marnewick et al. 2008)
- red fox *Vulpes vulpes* (Sarmento et al. 2009)
- maned wolf *Chrysocyon brachyurus* (Trolle et al. 2006)
- spectacled bear *Tremarctos ornatus* (Ríos-Uzeda 2007)
- wolverines *Gulo gulo* (Royle et al. 2011a)
- crab-eating raccoons *Procyon cancrivorous* (Arispe et al. 2008)
- common genets *Genetta genetta* (Sarmento et al. 2010)
- Malagasy civets *Fossa fossana* (Gerber et al. 2010, 2012)
- lowland tapir *Tapirus terrestris* and Asian tapir *T. indicus* (Montenegro 1999, Holden et al. 2003, Noss et al. 2003, Trolle et al. 2008)
- desert bighorn sheep *Ovis canadensis mexicana* (Perry et al. 2010)
- giant armadillo *Priodontes maximus* (Noss et al. 2004)

Jaguars *Panthera onca* have been the subject of many camera trapping studies (e.g. Maffei et al. 2002, Kelly 2003, Wallace et al. 2003, Maffei et al. 2004, Silver et al. 2004, Cullen et al. 2005, Soisalo & Cavalcanti 2006, Ceballos et al. 2007, Salom-Pérez et al. 2007, Paviolo et al. 2008, de la Torre & Medellín 2011). To date, the Wildlife Conservation Society has supported in part or full at least 84 different camera trapping efforts across 14 countries (Maffei et al. 2011a*)*. The total number of jaguar surveys is even higher, and they extend from the species' northernmost limits in Arizona to its current southern bounds in northern Argentina.

The extent of jaguar range yet occupied (~47% of the species' historic range), the large size of jaguar conservation units or JCUs (e.g. 25,000-100,000 km^2) (Sanderson et al. 2002, Zeller 2007), low human population densities in comparison to India, with correspondingly less transportation infrastructure, has meant that the genesis of camera-trapping for jaguars occurred in quite different environments than where surveys have been conducted on tigers. Some jaguar habitats provide very challenging access logistics, which in the past have influenced study design, though they should not in the future. Jaguar study areas can range from vehicle accessible areas through places which require three to five days river travel in dugout canoes to simply reach the study site.

Yet, the principles of study design and data analysis remain the same no matter the logistical challenges. That is one of the justifications for this manual.

A paper by Silver et al. (2004) and Scott Silver's (2004) manual informed a generation of jaguar camera trappers. However, in the last years following camera trap technology has advanced, new analytical models have become available, and experience has informed us on how we can improve our efforts at jaguar population estimation. The purpose of this manual is to convey recent advances and provide guidance on the basics for those conducting jaguar surveys for the first time.

The objective of a mark-recapture (or in this case, photograph/re-photograph) study is to estimate the number of individuals within a sample area. In basic terms, this estimate is generated by first estimating capture probability based on the capture histories of animals photographed. The number of animals in the sampled area is then estimated by dividing the total number of animals caught by the estimated probability of catching an animal at least once. The technique does not have to be based on a non-random sampling of the area, i.e., the cameras are set up in a pattern designed to maximize capture probability for all animals in the sampled area. The more individuals of the target species that are photographed, and the more often each individual can be photographed, the more robust the resulting abundance estimate.

When White et al. (1982) developed the method for small mammals, they recommended a minimum of 75-100 individuals, 20 recaptures, and a capture probability of 0.30. In camera trap surveys for jaguars, between 2 and 27 individuals have been identified, but most surveys have recorded less than 10 individuals. The number of individuals can be increased by enlarging the camera trap polygon, but the upper limits of this expansion can be constrained by logistics and costs, which mean that detecting 75-100 individuals is impossible in practical terms. Caution is warranted for the density estimates generated by extremely small samples (Maffei et al. 2011b). Recent spatially explicit capture-recapture models more successfully address problems posed by individual heterogeneity in capture probabilities in conventional capture-recapture analyses, and offer non-asymptotic inferences which are more appropriate for small samples of capture data typical of photo-capture studies (Gopalaswamy et al. 2011).

Reviews of past jaguar surveys and subsequent recommendations for surveys are presented in Maffei et al. (2011a, 2011b), Foster and Harmsen (2012), Noss et al. (2012) and Tobler and Powell (2013).

In the course of 10 years of jaguar camera trapping we have learned to distinguish between: 1) studies that are exploratory in nature assessing the presence of jaguars in area: 2) studies intended to use data as indices to compare relative abundance across threat levels, or habitat types, or land use prescriptions, or even time; 3) studies intended to generate an unbiased and precise and thus accurate estimate of jaguar population density in the sample area. All three objectives are legitimate and a contribution to the collective knowledge about jaguar distribution and abundance. However, the third objective has a particularly demanding set of requirements to generate a quality estimate. Of the three, the latter requires the most care in preparation, and should not be attempted unless adequate time, resources, and equipment will allow the rigorous sampling needed.

This protocol should be viewed as a living document. Technological and analytical innovations will likely result in methodological changes and modifications to analytical techniques.

Sampling in the Upper Caura watershed, Guianan Shield Forests,Venezuela.
Photo by Lucy Perera

CHAPTER I

GETTING STARTED

Before beginning any research project, investigators should have a clear idea of what information they need to help them address their primary conservation issue or question. Before investing in a photographic recapture survey, researchers should be certain that abundance or density is a quantity that will really be of use to them. To carry out an abundance estimate based upon photograph/re-photograph ratios (hereafter referred to as 'camera trap estimates') the research team must have certain information and equipment.

Minimal requirements:

1) maps or geographic knowledge of the study area.
2) access to the study area and a means of traveling throughout the study area.
3) a rudimentary idea as to the topographic features of areas inhabited or sites visited by the study animal, and their travel routes.
4) enough people familiar with the function and maintenance of camera traps to deploy and monitor the traps in a timely fashion.
5) a sufficient number of camera traps to photograph (i.e., "capture") enough individuals of the target species to generate a statistical estimate of abundance. If a rigorous population estimate is the objective, this is a serious requirement for reasons elaborated in following sections.

Additionally, it helps to have:

1) someone with a high degree of familiarity with the study area.
2) existing trails or roads to facilitate access to the study area.
3) extra camera traps to act as replacements in the event of equipment failure.
4) a thumb nail estimate of capture rates for the target species.
5) rough estimates of home range size and life history information.
6) hand-held GPS units.

BEFORE YOU DEPLOY THE CAMERAS, DO A PILOT STUDY !

As with most research projects the value of a pilot study for camera trapping cannot be overstated. The advantages include:

- Familiarity with equipment – A pilot study can reduce the loss of valuable data through faulty set up and deployment of camera traps. Practicing with your equipment in the study area helps minimize mistakes such as setting up cameras facing the wrong direction relative to the animal's route of travel, or pictures that fail to photograph clearly identifiable marks because the camera is too close, too far away, or at a poor angle.

- Realistic assessment of capture success rate – This helps the researcher to estimate how many cameras and how large an area is needed to sample in order to collect enough data for the mark-recapture analysis.

- Realistic assessment of monitoring effort – Depending on the type of equipment being used, the rate at which the memory cards / batteries / lures need replacement depends upon a number of factors. By establishing how many animals (both target and non-target species) are photographed and how long batteries function under your particular field conditions, it can be estimated how often you need to visit the cameras for routine maintenance. You will also be able to estimate the rate of equipment failure.

- Training of field assistants – Even if the principal investigator is familiar with the use of the camera traps, a trial period allows other project personnel to develop a sufficient level of expertise in their use. It also familiarizes the research team with the required logistics of deployment and monitoring, and ensures that sickness or injury to the principal investigator does not result in the failure of the survey.

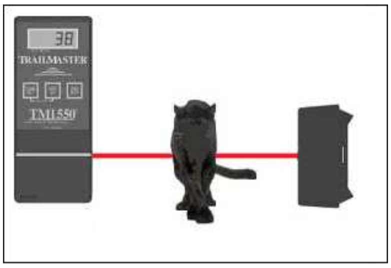
In summary, a pilot study will ensure that when you come to conducting a formal survey, you will maximize the number of captures of the target species. This increases the accuracy of the abundance estimate, while saving time, effort, and resources.

BEFORE THE FIELD

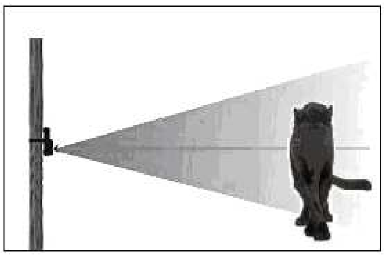
Camera Selection

The field research described in this document depends on camera traps that are triggered by an animal. Camera traps can be grouped into two broad categories, active or passive, based upon their triggering mechanism.

Active traps: Active traps take a picture when an animal or object crosses an infra-red beam. These cameras rarely miss target animals, but are prone to false captures for example, from wind-blown leaves and rain drops. Particularly windy or rainy days can expend entire rolls of film / memory cards on non-target images.



Passive traps: These are triggered when an object with a different temperature than the ambient temperature moves within the camera's detection zone. These cameras are less prone to false captures, but are more prone to "heat blindness" when high ambient temperatures approach mammalian body temperatures. Direct sunlight compounds this problem.



Traditionally, camera traps used film. Most camera trap suppliers no longer produce film cameras, thereby obligating researchers to use digital camera traps. The ability to eliminate film, which was often damaged by rain, or became stuck due to humidity means the pressure to re-visit the units is less urgent, but not absent. Equipment can fail and must be checked. However, new digital camera traps can operate for lengthy periods with minimal battery draw-down and with considerable memory left in the SD cards which are collecting data. For remote areas, with some study areas literally days from the nearest road, this is a huge advance. Criteria to look for in digital cameras include: 1) fast shutter speed both day and night (less blur and better identification of individuals); 2) night flashes which balance illumination with desired range – neither "washing out spots" with too much flash, nor missing identifications of individual cats a bit further out due to inadequate flash: 3) capacity to take serial photographs with one event – since cats are mobile and identification through spot patterns is the goal, the more photographs from the maximum angles possible of that cat at that time, the less missed opportunities for identification. We have found that digital camera traps capable of recording a rapid sequence of photographs and the standardized application on a local attractant (e.g., Calvin Klein's Obsession for Men) can both cause the jaguars to linger in front of the camera, and maximize the opportunities for adequate photographs from multiple angles to identify the individuals (Isasi-Catalá 2012, Maffei et al. 2011b, Moreira Ramírez et al. 2011).

As different camera trap models have different features and designs, the choice of a model is often dictated by the particular characteristics of the individual study (Swann et al. 2011). Here is a partial list of considerations for choosing camera traps:

- *Cost* – Currently, digital camera traps range from about $150-$650. With anywhere from 60-100 traps required for a rigorous jaguar abundance survey, financial requirements can vary tremendously. However, good equipment usually pays for itself over the long term. An investment of $250-450 per unit may be inevitable for quality equipment

- *Camera characteristics* – These can vary significantly across models and will affect number and quality of photographs obtained: shutter speed, storage capacity, battery life, and monochrome infrared vs. color photographs. The sensor quality is the most important feature, maximizing the photographs of any animals passing in front of the cameras, whereas the photos adequate for individual identification (of spotted / striped animals) need not be publication quality.

- *Technical expertise* – Most camera trap models today require considerable expertise for proper use, for example to program them initially and to re-program them in the field should they fail. Consider the level of expertise and experience required for whoever will be deploying and monitoring the cameras in the field. For example, downloading memory cards in the field requires more expertise and equipment than simply replacing memory cards when cameras are checked.

- *Monitoring ability* – When accessibility to camera traps is limited, visits to monitor cameras may be less frequent, and researchers need to consider battery life, memory card life, and camera trap weight. We recommend carrying at least one replacement unit for all trips to monitor cameras. For long trips to many stations, you may need to carry more than one replacement. If it is necessary to carry the units long distances, larger and heavier units may be less desirable.

- *Site security* – Although it is virtually impossible to stop a determined camera trap thief, some models possess anti-theft features that enable them to be locked. The most secure designs typically comprise a full metal case with a tamper-proof means of anchoring it to a tree. If your site is secure from theft and mischief, there are models with no anti-theft features, resulting in reduced weight. If the site is near communities, you can reduce risk by hiring community members as field technicians who check the camera traps and also inform other residents about the study (a successful approach in the Maya Biosphere Reserve, Guatemala).

- *Weather* – Most camera trap brand models are in self contained, weatherproof units. Even amongst water-resistant models, some can be completely submerged, while others have sensors that are vulnerable to immersion and flooding. Across much of the jaguar's range, a unit's ability to withstand high humidity and even heavy rainfall can be a critical consideration for a successful survey.

- *Access to technical support* – Ask other users about their experiences with manufacturer support. What is their warranty policy, how much do repairs cost, are they accessible by phone, and what is their turn-around time for replacements and repairs? All of these considerations can make a significant difference to the number of camera traps that remain functioning under field conditions.

Designing the survey

Since camera traps are used to collect data on a number of topics, including species diversity, species presence, wildlife use of key resources, habitat use, and activity patterns (Maffei et al. 2002, Arispe 2007), each of these objectives should guide a particular survey design. A good design for one objective will not necessarily be the best design for another. We focus below on systematic camera trap surveys used to estimate population abundance and density by applying capture-recapture analytical methods.

- Abundance

For the purpose of abundance estimation, detection probability can be defined as the likelihood that an individual will be detected (photographed or captured) if it is present in a sample unit during the time of the sample. Detection is a source of variability in abundance estimation because not all animals will be detected with absolute certainty during a sampling effort, individuals may vary in their detectability and detection may vary over time and space. The likelihood of detecting an individual during a sample occasion provides the key to *converting the sample count statistic into an estimate of abundance or density. Detection probabilities therefore are an important component of any abundance estimation exercise or monitoring program (O'Brien 2011).*

- The assumptions of mark-recapture

Two critical assumptions need to be satisfied when designing a mark-recapture camera trap survey. These assumptions are discussed in detail in Karanth and Nichols (1998) and summarized below.

Population closure: The mark-recapture model is based upon a closed population i.e., no births, deaths, immigration or emigration of individuals within the study area during the survey (O'Brien 2011). In reality few jaguar populations are actually closed, so in practice the assumption is satisfied by limiting the duration of the survey. The longer the survey is, the greater the likelihood there is of violating this assumption. Based upon the life history characteristics of tigers, Karanth and Nichols (1998) concluded that three months was a reasonable time-frame to assume a closed population. Similarly surveys on African leopards have typically used two to three months (Henschel & Ray 2003). Numerous jaguar surveys have used three months or less (Wallace et al. 2003; Silver et al. 2004; Maffei et al. 2004, 2011a, 2011b) as a data collection period.

All individuals have non-zero capture probability: The second important assumption is that every individual inhabiting the study area has at least some probability of being photographed (i.e., there is at least one camera trap within its range during the duration of the survey). It is important to realize that not every jaguar in the study area needs to be photographed, but that every animal has some chance of being photographed. This assumption dictates how far apart your camera traps can be placed and determines the maximum size of a contiguous area within the study site without at least one camera trap. The camera stations can be as close as the researcher is inclined to set them, but there must not be gaps between camera stations large enough to encompass a jaguar's home range. A conservative approach to satisfying this assumption is to adopt the smallest home range estimate documented for your target species in your habitat and/or geographic region, as the minimum area within which there must be at least one camera station. Once that minimum area is known, calculate the diameter of a circle with that area. This diameter is the maximum allowable straight-line distance between camera stations.

Female home ranges are generally smaller than male home ranges (Cavalcanti and Gese 20009, Crawshaw and Quigley 1991, Rabinowitz and Nottingham 1986, Scognamillo et al. 2003). Initially recommendations for space between stations were based on an extremely small home range of 10km² recorded in Belize (Rabinowitz and Nottingham 1986). Despite the validity of that record, drawing from wider range of estimates of 10-65 km² recorded in Mesoamerica would generate diameters of 3.2-8.1 km (Maffei et al. 2011b). Home ranges recorded in South America have tended to be larger, with male ranges frequently over 100km² (Scognamillo et al. 2003, Cavalcanti and Gese 2009) and sometimes several hundred square kilometers in size (Tobler and Powell 2013). Low density populations demand large sample areas and urges wider spacing. In general, wider spacing will allow more animals to be caught, facilitate a larger sampling area, and is encouraged. The caveat is that females who have recently given birth and with small cubs use miniature areas (Farrell 1999), which expand with time.

The tension between sampling a huge area with widely spaced camera trap stations, and spacing stations close enough to maintain the probability of all animals being captured at >0, means that studies must aim for a compromise. Sollman et al. (2011) deployed a grid with maximum distances of 3.5km between stations in an area of extremely low densities in Brazil, while Tobler and Powell (2013) suggested spacing as wide as 4 or 5km based on circular home ranges of 50 and 80km², the former of which appears to be a biologically reasonable maximum based on female home ranges in Venezuela and Brazil (Cavalcanti and Gese 2009, Crawshaw and Quigley 1991, Scognamillo et al 2003). It is acceptable to miss some individuals, as analytical methods are based on detection probability, but each individual should have some possibility of being captured.

-Planning the survey area and duration

An example of a camera deployment design is shown in Figure 1. In the Kaa Iya landscape in Bolivia, camera spacing of 2-4 km was used for jaguars and pumas (whose ranging behavior is unknown in this landscape), versus spacing of 1 km for ocelots and tapir (consistent with home range information for these two species derived from telemetry research within the landscape).

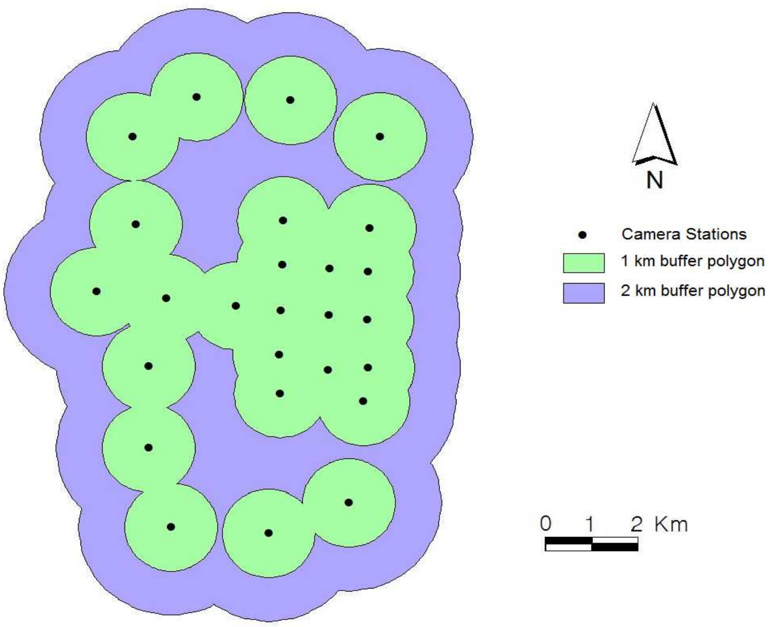


Figure 1: Tucavaca II (2004) camera trap deployment for tapirs and ocelots (green polygons, 1 km spacing) and jaguars / pumas (blue polygon, 2 km spacing).

While there is no set minimum distance between stations, a survey will not be meaningful if all cameras are concentrated in a very small area that will only capture a few individual animals nor will it be representative of any larger area of interest if it focuses on a known concentration area. Jaguars are at the top of a trophic chain in habitats in which the biomass of terrestrial prey is often low. They must cover large areas to survive, and the lower the biomass of prey, the larger the home ranges. Numerous issues arise when a survey sample area is too small, including bias which can lead to overestimates.

Surveys should include areas much greater than the home range of a single jaguar as one cannot estimate population density by sampling at the scale of one animal. Radio-telemetry studies in Central America reported home ranges as small as 10-40 km^2 (Rabinowitz & Nottingham 1986) in Belize, but also larger, such as 32-59 km^2 (Ceballos et al. 2002), and 25-65 km^2 (Nuñez et al. 2002) in Mexico. Larger home range estimates can be expected from the next generation of telemetry studies in Central America. Home range estimates from South America have been larger, such as 51-108 km^2 in Venezuela (Scognamillo et al. 2003), and 34-263 km^2 in similar habitats in Brazil (Cavalcanti 2008, Cavalcanti & Gese 2009). The lower end is females, the larger ranges are males. Unpublished estimates from colleagues in other study areas in South America have female ranges in excess of 300 km^2 and male ranges larger than that.

In simulations which varied home range estimates, numbers of camera trap stations, sample area (camera trap station polygons) Tobler and Powell (2013) observed large positive bias (overestimates) when camera trap polygons were small compared to home range estimates, but that simulations using sex covariates (separate male and female home range estimates) were unbiased when the camera trap survey polygon was equal to or larger than the size of one male's home range, noting that in the Pantanal of Brazil a polygon of 200-300km^2 (Cavalcanti and Gese 2009) might be sufficient. Their results still suggest, in areas with low jaguar densities (<2 jaguar 100 km^2), the camera polygon might need to cover several home ranges in order to produce reliable estimates.

Our recommendation of large sample areas focuses on males. Small female ranges guide the maximum spacing between stations. Noting the smallest home range size of jaguars in the Cockscomb Basin of Belize, Silver (2004) suggested 10 km2 as a maximum gap area allowed between camera stations, with 3.6 km (the diameter of a circle with an area of 10 km2) as the maximum straight line distance between cameras. This recommendation is safer when using the home range radius, but fortunately female home ranges in most areas are larger than 10km^2. Tobler and Powell's (2013) simulations found the maximum spacing which gave accurate results was about one half the diameter of a home range. The following is offered for the reader's convenience.
Home range: 10km^2, radius 1,783m, diameter 3,567m, ½ HR 1.8km
Home range: 20km^2, radius 2,523m diameter 5,046m, ½ HR = 2.5km
Home range: 25km^2 radius 2,820m, diameter 5,640m, ½ HR = 2.8km
Home range: 30 sq km radius 3,090m diameter 6,160m, ½ HR = 3km
Home range: 50km^2 radius 3.989m, diameter 7,978m, ½ HR = 4km
Home range: 80km^2 radius 5,046m diameter 10,092m, ½ HR = 5km
Home range: 100km^2 radius 5,642m, diameter 11,284m,
Home range: 140km^2 radius 6,676m, diameter 13,351m,
Home range: 200km^2 radius 7,979m diameter 15,958m

Tobler and Powell (2013) found asymmetrical camera grid layouts reduced bias with density estimates *started* to be unbiased when the longest side of the camera grid equaled one home range diameter. The model used in these simulations used perfectly round home ranges. Since home ranges may be elliptical or irregular, this fascinating result merits testing with field data.

If an accurate density estimate is the goal, samples must exceed estimated average male home range. If equipment and logistics force small sample areas, then the survey falls more into the spectrum of exploratory work, or an index based on number of individuals detected per effort (time and space), rather than a density estimate study.

Given current telemetry based knowledge on jaguar home ranges in Central American forests, we recommend that the polygon formed by the camera traps should cover a minimum of 120 km² (Maffei et al. 2011b). The observation that a minimum of 45 camera stations is required to cover a polygon of 120 km^2 at 2km versus 20 stations at 3km spacing demonstrates how spacing of units relates to equipment needs. Tobler & Powell (2013) suggest a minimum of 40 – 50 stations. When numbers of camera traps is limited, shifting the cameras across two or three blocks can help attain the size needed for a representative sample. In South America, where larger home ranges have been recorded jaguar surveys should strive to cover 500–600 km^2 and at the very minimum camera trap station polygons should be approaching 300 km² (Maffei et al. 2011a, 2011b). Tobler and Powell (2013) recommended polygons of 500-1000km², which is scientifically valid, even if challenging logistically and financially.

There is no set minimum time for a mark and recapture study as long as the sample provides adequate capture-recapture histories to generate a capture probability based estimate with scant bias and high precision. Typically low jaguar densities challenge those goals. Based on field experience we have recommended minimal sample periods of 45-60 days for a single block survey, and nothing shorter than around 30 days when sequential blocks are employed. Because of their wide ranging movements in search for productive areas of prey, even resident cats may cover considerable distances, with revisits to specific places potentially spaced at 7-10 day intervals. Given that possibility, it has seemed sensible to allow enough time to capture those revisits in that general area, even if the total sample area may capture those cats elsewhere. Study duration is a trade off based on resources, but less with current digital units than it was with the first generation of film cameras which required more frequent visits. Simulations run by Tobler & Powell (2013) resulted in reduced precision for a 30 day sampling period, and the authors recommended a minimum of 60 days when densities and encounter rates were high, or when sequential adjacent blocks were used, suggesting data gained by longer sample periods (e.g. 90 days and more) justified the risk of violating the assumption of population closure.

If the number of cameras is limited, the size of the trapping area can be increased as follows. Design two trapping patterns (i.e., “grids”) adjacent to each other and deploy them in two consecutive data collection periods. Using the full complement of cameras, collect data in the first grid for a ‘sub-sample’ of the entire survey duration (e.g., 5 weeks), then move the cameras to the second grid, for the same amount of time (in this case, 5 weeks for a total survey duration of 10 weeks). When analyzing the data, treat the resulting data set as if both grids were run simultaneously, even though they were not. All jaguars photographed on the first day of either grid are treated as photographed on Day 1; those photographed on Day 2 of either grid are treated as photographed on

Day 2, etc. Animals photographed on different days are considered recaptures. This technique can be repeated again if necessary (i.e., additional grids incorporated), and the data analyzed the same way but take care to limit the total survey duration within the time required to satisfy the population closure assumption

> *When attempting to make inference about a large area, it is rarely possible to sample the entire area of interest, and investigators should take care to select locations for sampling arrays that are representative of the area for which inferences are made. If the investigator wishes to make inferences beyond the effective sampling area (e.g., extend the inference from a sampling area to an entire park), then rules of stratification or random sampling should apply in determining the location of a sampling array. Often, sampling areas are chosen because they appear to be typical of the larger area of interest, or because they are easy to access. Representativeness, however, is not easy to assess subjectively and easily accessible areas often are not typical of areas that are not easily accessed (O'Brien* 2011).

Fine-tuning the design

Once you have established your basic design that satisfies the assumptions, you need to fine-tune the placement of the camera traps. Remember, camera placement is not necessarily random nor strictly systematic. Camera station locations should be selected to maximize the capture probabilities of individual target animals in the study area, while covering as large an area as possible to maximize the number of individuals photographed. This is a balance between positioning cameras closely enough to satisfy the assumption of all animals having a nonzero capture probability (as described above), and covering a large enough area to photograph more individual jaguars. It is also desirable for the animals in the study area to have similar capture probabilities, to the extent possible. While there are ways to account for variable probability of capture, estimations are simpler and more precise when capture probabilities are similar amongst animals. Because of this, try to maintain a comparable density of camera traps throughout the sample area. The idea of placing many cameras within one animal's home range, while placing only a single camera within the range of another, should be avoided.

To plan your sampling design, begin with a topographic map of the study area. Mark sites with a high likelihood of photographing the target species, for example established trails or dirt roads in the case of jaguars and other cats. Space them as far apart as possible without missing promising locations, or without violating the assumption of geographic closure. Remember the cameras will have to be monitored, so keep in mind the logistical limitations of your design.

After the ideal camera trap locations have been selected on the map, look for gaps among camera trap locations greater than the permitted gap size, and either add camera stations to fill in those gaps, or shift some of the existing sites closer together. Some camera stations may have to be located in areas with little or no animal sign, but do not deploy units where you know target animals will not go (e.g., very steep slopes).

Deploying camera traps and following tracks in Venezuela in 1998, Polisar noted that males seemed to walk more length down open and semi-open dirt roads than females which were more frequently photographed on smaller trails in forests. Many surveys across a variety of sites have used the jaguar's trait of seeking clear pathways to maximize capture probabilities (see Maffei et al. 2004, Harmsen 2006), leading Maffei et al. (2011b) andTobler and Powell (2013 a,b) to recommend that abandoned roads and foot trails be used. Conde et al. 2010 found habitat differences between males and females in the Maya forest of southern Mexico, including road avoidance by females. The subtleties of differential road and trail use by genders, if extant and measurable, remain to be adequately quantified.

New trails may need to be cut to establish some camera stations/maximize captures, but if possible this should be done several months ahead of the survey so that animals become accustomed to using them (Arispe 2007, Maffei et al. 2011b). In some areas it is important to consider the expected benefits of these new trails for the research project versus the possible costs if these trails facilitate access for hunters.

Record the exact coordinates of these predetermined camera trap locations. For the purposes of this document, these locations are called your 'predetermined coordinates'. These act as your general guide to camera placement but the ultimate position may differ slightly when you go to the field (explained in the next section).

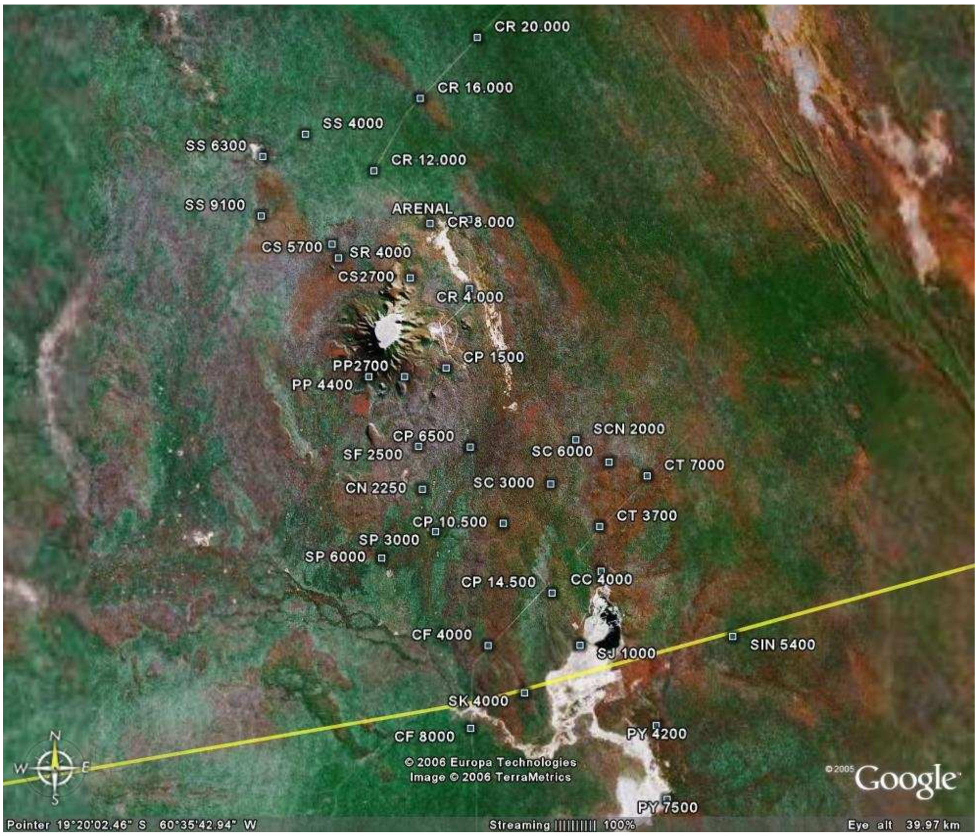


Figure 2. Camera trap deployment in the Palmar-Ravelo mega-survey (Dec. 2006-Mar. 2007) (Google Earth). The majority of camera trap locations were along roads or trails, and spacing is 2-4 km for jaguars, with a camera polygon of 434 km^2 (Montaño et al. 2010).

CHAPTER II

CAMERA DEPLOYMENT IN THE FIELD

Before you deploy the cameras

Film / memory cards: It is critically important that every roll of film / memory card is labeled with the date of deployment and camera number (corresponding to the camera's location) before the cameras are placed in the field. When the film / memory cards are collected and developed, you may have dozens of rolls / memory cards from 20-30 different locations.

It is vital that you know the location of all your photographs in order to undertake spatially-explicit capture-recapture analyses (see below).

Date & time settings: Photographs are useless without an accurate date and time stamp. The date on the photograph is essential for determining the individual capture event. Each 24-hour period can be considered a different event so that all pictures of an individual photographed on the same date are considered a single capture.

While camera models may differ slightly in setting the time/date stamp the important consideration is that it is consistent among all cameras in the survey. When the set up functions allow you to enter a station name and camera ID, or coordinates, do so, because these labels are another way to ensure organized data.

Time delays: All camera traps can be programmed with a delay between successive pictures. This is important as groups of tourists, herds of peccaries, or other non-target animals can result in many wasted pictures and in the case of film cameras, expend film before the survey is finished. A camera that is out of film / memory creates a data gap in the survey design that may result in the loss of all data for that time. The delay setting should be based upon the likelihood of encountering large groups of non-target animals: experimentation during the pilot study period will assist in selecting the length of the delay setting for your study site. Because a longer delay increases the probability of missing a capture, the rule of thumb should be to use the minimum length of delay with which you feel comfortable.

Each camera trap site (known as a camera station) should contain two cameras on either side of the trail, stream, or road, aimed at a perpendicular angle to the target animals' presumed direction of travel. It is recommended that you always incorporate two cameras per station to ensure pictures are taken of both sides of the target animals (to ensure identification from a single capture event) and supply a level of redundancy in case of camera failure.

Choosing the camera trap site

In the field, the researcher needs to find the best possible location as close as possible to the predetermined coordinates. The exact site is chosen to give the highest probability of obtaining useful photographs whenever a target animal passes by. The goal is to photograph both flanks of the animal, since this is the area where the individual markings are easiest to distinguish.

Once in the vicinity of the predetermined coordinates, search for the nearest location with a good chance of visitation by the target animal. For example, features such as trails, dirt roads, river banks, beaches, and game paths to water are all used regularly by jaguars and other cats. Look for sign (tracks, scrapes, scats / dung, or past sightings) nearby. Generally, if there is any sign even a few kilometers away on the same trail, the entire path is probably used by the target species.

- Try to determine the travel path of the target animal – Pick a site where the target animal's travel path is limited to the area that can be photographed by the cameras. For example, a place where there is a good deal of sign, but with several different trails crossing in close proximity to each other would not be a good location to place camera traps. If there is more than one trail going in different directions, you are less likely to be able to predict which trail the animal will travel, and it will be difficult to aim the cameras perpendicular to the animal's direction of travel. Similarly, a wide-open area is a poor choice because animals may cross it at any point and be traveling in any direction. A single trail with evidence of use by the target species and limited travel alternatives is optimal for placing cameras.

- Consider the camera's field of view – A wide trail has more places in which the target animal can cross a sensor and the greater the area that must be covered by the camera's field of view. Remember, good pictures from both cameras are desired. The maximum distance separating the cameras should not be further than the distance covered by the flash.

- Consider the terrain – The ground under the sensor beam needs to be reasonably even. Trails with ruts or slopes can result in the ground obscuring a traveling animal from one of the sensor beams, and might cause the trap to miss photographs. A path with a pronounced slope on one side of the path can result in a sensor beam that is at shoulder height when the target animal walks on the upside of the path, but misses the animal entirely if it walks on the down slope of the path. Be aware of all the possibilities of travel in front of the cameras.

- Many studies have recorded more males than females (Maffei et al. 2011b). While males are more mobile than females and thus more often photographed, there may be a risk of biasing all the camera trap stations towards travel routes preferred by males. Conde et al. (2010) found significant habitat differences with males using relatively open areas with greater frequency, whereas females preferred thicker cover and avoided roads. These findings complement the suggestions of Sollman (2011), Tobler and Powell (2013a), and Tobler et al. (2013)'s suggestions that gender specific differences (in home range size) merit separate models for males and females. However, though Foster et al. (2010) suspected differences habitats between genders, they found no significant differences. The recommendation to counter this ambiguity about open roads and narrow trails as a factor distinguishing male and female captures is to attempt a balance between good camera viewing fields with adequate cover nearby, and including a diversity of micro-site types in the sample.

Setting the camera traps

Once all these factors have been considered, the camera traps must be set.

- Find a spot where there are two suitable trees or posts on opposite sides of a trail. Suitable trees have trunks that are reasonably straight, thin enough to tie a chain or wire around, but not so thin that wind, people or other animals can shake it excessively. In the case of passive traps, try to minimize direct sunlight on the cameras as excessive heat can reduce the sensitivity of the sensors to endothermic animals. Cameras should be set back at least two meters from the nearest point where a target animal might travel across the sensor. This allows for clear, focused pictures and a large enough field of detection from the sensor. The longer the target animal is in the detection zone, the less chance of missing a photograph. Because the sensor beam should be approximately shoulder high, for a jaguar the camera should be set approximately 50-70 centimeters off the ground and parallel to it. Both cameras should be faced slightly down the trail to prevent mutual interference, but aimed at approximately the same point.

- Use fresh cut sticks and branches to help prop up and secure the camera to the tree trunk or other anchor. A well-placed twig placed between the camera housing and the tree trunk can help adjust the angle in which the sensor is pointed. (Always use live wood to brace cameras and adjust camera angles, since dead wood is too brittle).

- Once the camera is set, clear the area between the camera and the path of travel of all vegetation that obstructs the beam reduces the detection ability of the camera, and could result in obscured pictures. Large leaves and wavy grass can result in false triggers when the sun heats up a frond blowing in the wind. Also try to avoid pointing the cameras at objects in direct sunlight that may absorb heat and trigger sensors such as large rocks or sunlit streams.

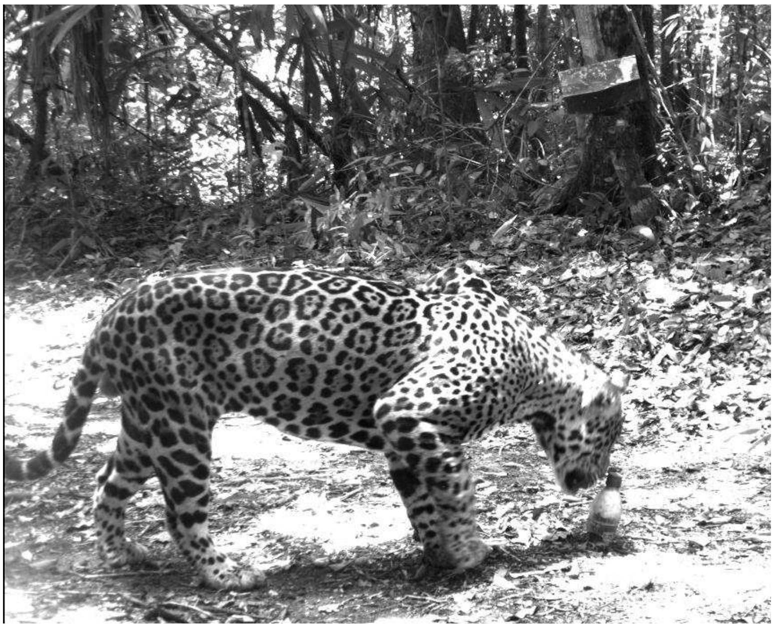
- Test the aim of both cameras by crossing in front of them. Do this on both the edges and the middle of the path. Most camera trap brands come equipped with an indicator light that will light up when the camera's sensor detects you. Approximate a target animal by walking in a crouch, and then walking in a more relaxed fashion. Make sure that every conceivable angle at which the target animal can pass in front of the camera is tested, and that in each instance a photograph is triggered.

Guido Ayala and Maria Vizcarra testing camera traps in Bolivia. Photo by Julie Maher

- Occasionally, limitations in terrain or suitable trees hamper complete coverage of a trail. In that case, lay brush or other obstructions down one side of the trail to influence where the target species will walk. This technique is also useful if you are unable to set the camera well back from the trail, and wish to deter a target animal from passing so closely to a camera that it cannot take a well-focused picture. Appropriate fencing can also keep livestock away from cameras while permitting target animals to pass (Rosas-Rosas 2006).

- Some studies have use scent attractants such as Calvin Klein's Obsession or Chanel N^{o} 5 (original or imitations) to lure jaguars in front of the camera traps. In the majority of cases case the perfume has sprayed on a piece of fabric or tampon attached to a stick, protected by a cut-off plastic bottle that prevents animals from removing the lure or rain from washing away the perfume, but allowing the scent to dissipate in the air. The stick is then fixed in the ground between the camera traps. The scent has been be replenished every week or 10 days. The lure probably does not draw animals from significant distances, but it can cause them to linger in front of the cameras, resulting in larger numbers of photos from various angles during each "capture" event, and thereby facilitating individual identification (Moreira Ramírez et al. 2011, Viscarra et al. 2011, García Anleu 2012).

- Isasi-Catalá (2012) deployed cotton impregnated with a commercial imitation of Chanel No.5, including tampons such as Tampax, contained within a small baby food jar with the top sealed with tape and the top punctured with fine holes to allow the odor to escape gradually. In the center of the camera trap station a shrub or small tree was retained with the jar affixed at approximately 1 m above the ground with the punctured top facing down to prevent water from entering. This prevented small animals from tampering with the jar, and a precise measurement of the height at which it was placed was useful as a reference for body size of visiting animals. Each time the station was visited the cotton was impregnated with scent again. By all appearances the scent caused the animals (a variety of species) to pause a moment in front of the camera traps, which facilitated identifications, with the interpretation that this scent helped position the animals, out of their curiosity in the lenses of the cameras.



Above: Jaguar and inverted bottle with scent in Nicaraguan Mosquitia, Bosawas Biosphere Reserve. Photo by Fabricio Diaz Santos. Below: Jaguar pausing to sniff in Maya Biosphere Reserve, Guatemala. Sheet metal roof design protecting camera from rain and scent application design courtesy of WCS Guatemala – R. Garcia, J. Moreira. Photo by Rony Garcia.

- Finally, don’t forget to have the exact GPS position of the camera just set.

Monitoring the cameras

The amount of traffic (both target and non-target species) and sensitivity of the trap brand will dictate how often the film / memory card needs checking. It is very important that cameras do not run out of film / memory during the study. The same is true of battery life. A proper pilot study will determine the safe interval between battery and film / memory card changes.

With current digital camera trap units, these concerns are much less severe than they were with the film units formerly deployed, yet it remains very important that all stations must be functioning throughout the study to meet all the assumptions of the study design. The ability to monitor the cameras sufficiently may be the limiting factor in how many stations are deployed. Be conservative when estimating how often film / memory cards and batteries need to be checked. Ensure that any film / memory cards removed from camera traps are immediately labeled with date, time, camera location, and camera unit. This information must in turn be recorded with every physical and digital photo from that film / memory card and in the databases constructed to store and analyze the data.

Don't forget:

LABEL YOUR FILM / MEMORY CARD WHEN REMOVED

Several surveys using camera traps in specific areas have not photographed jaguars despite documentation of individuals by other means. We can attribute these results to a number of issues: (1) camera failure, (2) low jaguar densities, (3) camera trapping period was not long enough to photograph an individual, and (4) lack of local knowledge about routes jaguars travel combined with a failure to place camera traps in such areas (Maffei et al. 2011a).

CHAPTER III

BACK IN THE OFFICE

Preparing and analyzing results

As the data are collected from each camera, ensure that it is properly labeled with the associated camera number and the date it was deployed. If developing film, ensure that the date and location are transferred to the developed photographs. Once all photographs have been collected, identify the individuals by comparing individual markings. Check your results against that of someone else looking at the same pictures. Record the date that each individual was photographed. Label each print or digital photograph with the camera number, location and the identification code of the individual.

Good record keeping at this stage is critical. Data can be managed in Excel files, where the simplest version contains at least the following information:

	A	B	C	D	E	F
1	**Species**	**Date**	**Hour**	**Place**	**Photo Number**	**ID**
2	Cerdocyon thous	28-oct-2011	23:58	Prog. 121.5	4797-0	-
3	Tapirus terrestris	28-oct-2011	22:45	Prog. 118,5	4251-0 / 4250-0	E3M
4	Cerdocyon thous	29-oct-2011	22:20	Prog. 121.5	4797-2	-
5	Panthera onca	29-oct-2011	22:58	Prog. 121,5	4244-2/4797-3	E2H
6	Tapirus terrestris	29-oct-2011	21:17	Prog. 118,5	4251-1 / 4250-2	E3M
7	Tapirus terrestris	29-oct-2011	00:09	Prog. 121,5	4244-1/4797-1	E3M

Where:
Species is the animal captured
Date is the date when the animal was photographed (marked on each photo)
Hour is the hour when the animal was photographed (marked on each photo too). Use always the 24-hour system.
Location is the place of the camera (usually with a easy to remember name, then linked to another database with the GPS position of each camera place)
Photo number is the number assigned to each photo in our database
ID is the identification of each individual identified by its natural marks.

For complementary analyses the user may wish to include additional columns on number of animals in the photo, sex, age, type of location, habitat type, etc.

Seeking to promote data consistency and sharing across sites around the world (see O'Brien et al. 2010), Tim O'Brien of WCS developed a more complex format in Excel with three linked worksheets. The first provides metadata for the dataset, program and project. The second provides information about each roll of film or memory card, including film number, film number pair, camera location, type of site, number of photos of wildlife / humans / domestic animals / vehicles / not used, coordinates, setup date and time, pickup date and time, date and time of last photo, number of trap-days, camera model. These data permit calculation of the survey effort as well as evaluations of camera effectiveness. The third worksheet, linked to the first two, provides for each frame the species name, date, time, number of individuals, age, sex, habitat, and the image ID.

With both of these types of Excel databases, the photos are managed separately, whether print, negative scan, or digital camera file. The researcher must therefore label each photo so that it can be cross-referenced with the corresponding data. In turn, input files for other programs (CAPTURE, MARK, PRESENCE, DENSITY, SPACECAP, secr) must be generated manually.

An alternative is the program Camera Base, developed by Mathias Tobler (San Diego Zoo Institute for Conservation Research). Versions 1.5 (Access 2003 / 2007) and 1.5.1 (Access 2010) can be downloaded free from http://www.atrium-biodiversity.org/tools/camerabase/. The program allows for batch-importation of photos from digital cameras, automatically reading date/time information from the EXIF data. The user must identify species and individuals including sex and age information in each photo, and the photos are linked to the data (location, date, time, habitat). In turn the program generates reports on number of photos and capture frequency for each species, activity patterns (hourly, day / night / crepuscular), and habitat use. It can also calculate the mean maximum distance moved (MMDM) for each species with individuals identified, and the user can run capture-recapture analysis in CAPTURE directly from Camera Base. In turn the program will mark each photo as an independent or dependent event based on a user-defined minimum time interval, and finally will export data in formats appropriate for input in MARK, PRESENCE, DENSITY, EstimateS and other statistical or GIS software.

Identification

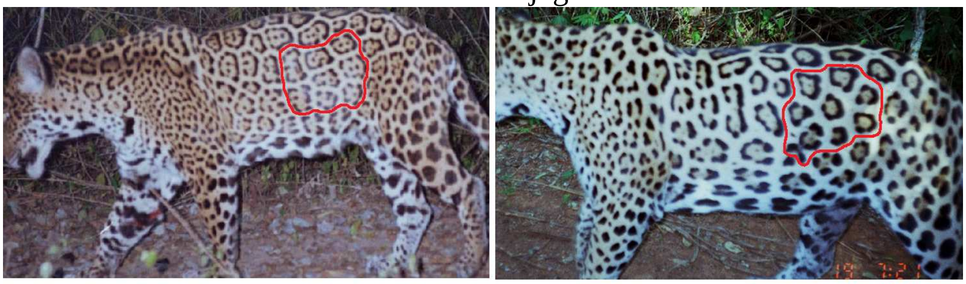
Identification of individual animals with spots or stripes (in the Kaa-Iya landscape jaguars *Panthera onca*, ocelots *Leopardus pardalis*, Geoffroy's cats *L. geoffroyi*, margays *L. wiedii*, and pacas *Cuniculus paca*) is straightforward, particularly when paired camera traps obtain photos of both flanks simultaneously (Arispe 2007). Tail spots and rings (number, width, full or partial rings) also facilitate identification in the case of the same cats and raccoons *Procyon cancrivorus* (Arispe et al. 2008, see Appendix 1 for tips on identifying several species).

IT IS IMPORTANT TO CHECK YOUR RESULTS AGAINST THAT OF SOMEONE ELSE LOOKING AT THE SAME PICTURES.

Identification of individual jaguars is straightforward, particularly when paired camera traps obtain photos of both flanks simultaneously (Arispe 2007). A number of software programs analyze population data through mark and recapture as well as other designs. An archive of such programs is maintained by the Patuxent Wildlife Research Center website at http://www.mbr-pwrc.usgs.gov/software.html, which provides a list of software programs and brief descriptions of them for the analysis of animal populations.

The same jaguar

Two different jaguars



The most commonly used software for generating closed population abundance estimates using camera photographs has been the program CAPTURE (Otis et al. 1978; White et al. 1982; Rexstad & Burnham, 1991). Its use jaguars use was presented in Silver (2004), its advantages and disadvantages discussed in Foster and Harmsen (2011), and its results compared to other models in Noss et al. (2012) and Tobler et al. (2013). This document provides a primer for two spatially explicit capture-recapture models as an update to Silver's (2004) CAPTURE focused primer.

Abundance indices: Camera trapping data of species non identifiable to individual level.

Systematic camera trapping surveys generate enormous datasets on non-target species including prey species for jaguars. As they have done for jaguars, researchers have used such data opportunistically to describe abundance, activity patterns, and habitat use by these species. Researchers have also used datasets from systematic camera trap surveys to compare jaguars / carnivores with and prey species in terms of their abundance / density, activity patterns, or habitat use (Griffiths & van Schaik 1993, Laidlaw & Noordin 1998, Maffei et al. 2003, O'Brien et al. 2003, Trolle 2003, Kawanishi & Sunquist 2004, Johnson et al. 2006, Weckel et al. 2006, Bowkett et al. 2007, Boas Goulart et al. 2009, Araguillín et al. 2010, Harmsen et al. 2010b, McCarthy et al. 2010, Montaño et al. 2010, Espinosa-Andrade 2012). As with jaguar datasets, the data can be stored and analyzed using Excel or Access database managers such as Mathias Tobler's Camera Base described in the text (for an application, see Tobler et al. 2008a).

In most cases, researchers have used abundance indices such as captures / 1000 trap nights (considering records one hour or one day apart at the same camera station to be independent observations of the species) in order to compare prey species with jaguars, prey species among each other, or prey species across sites and years. In some cases researchers have used captures / 100 trap nights (Díaz-Pulido and Payán Garrido 2012). Capture frequency, expressed as captures /1000 trap nights (Gerber et al. 2010, O'Brien et al. 2010, Jenks et al. 2011), is calculated as number of photos from a given species multiplied by 1000 and divided by the total trap nights during the survey (# of camera trap stations X length of the survey in days).

One drawback to this type of index is that it does not distinguish few individuals photographed many times from many individuals photographed few times each. A single photo of a prey species that usually lives in groups, such as peccaries, includes many fewer visible individuals than are present. Extensive complementary information from the study area is required, such as group size in order to better approximate densities and biomass based on camera trap records for these species.

> *Carbone et al. (2001) argued that photographic capture rates (photo captures per unit time) could be used as an index of density for species that cannot be individually identified. However, this requires describing and calibrating the relationship between capture rate and density, and measuring the precision of the calibration (*Jennelle et al. 2002, Foster & Harmsen 2012).

A survey designed for jaguars will choose sites seeking to maximize captures of jaguars, not to maximize captures of the diverse array of prey species upon which jaguars depend, nor to ensure a random survey across the study area. Studies have therefore found significant differences in capture rates for prey species on roads versus trails (Trolle & Kéry 2005, Weckel et al. 2006). Camera traps situated to maximize jaguar captures may miss entirely particular micro-habitats or specific locations within the study area that particular prey species frequent. Jaguars in some areas depend heavily on aquatic or semi-aquatic species such as turtles and caimans, or semi-arboreal species which may be are absent or rare in camera trap surveys (Cavalcanti and Gese 2010, Emmons 1987, Emmons 1989, O'Brien et al. 2010, Polisar et al. 2003, Weckel et al. 2006,). In addition to using animal trails (Weckel et al. 2006), some surveys have placed cameras at salt licks (Maffei et al. 2003, Araguillín et al. 2010) and waterholes. All these can record prey species, but with potential bias that: 1) must be recognized; and 2) is difficult to measure. For example, salt licks tend to attract ungulates much more than other prey species, thus abundance of these species may be overestimated. Comparison of data from roads / trails with salt licks is therefore complicated.

Mathias Tobler and colleagues summarized some of the constraints in drawing conclusions from comparisons of capture frequencies across species:

> *We believe that capture frequencies are a relatively poor index for relative abundance among surveys or for comparing relative abundance of species within surveys because of a variety of factors such as species-specific behavior [e.g. use or avoidance of trails…, partly arboreal versus exclusively terrestrial, or habitat specialist versus generalist], species size (large animals are more likely to trigger the cameras), home range size (animals with larger home ranges move around more and have more cameras within their home ranges) or simply stochastic variation as can*

> *be seen when looking at the large differences in capture frequencies for several species.* (Tobler et al. 2008a).

Foster and Harmsen (2012) cautioned against using surveys designed for one species for other species which may use habitats quite differently:

> *Using the same survey design for multiple species may produce imprecise density estimates because the optimal trap location, spacing, and minimum survey area for one species may not be optimal for another species…. Inter-specific variation in capture rate may reflect a difference in abundance or detection probability between the species (or a combination of both).* (Foster & Harmsen 2012).

Because of these caveats, Tobler et al. (2008b) and O'Brien (2010) stated that:

> *Capture frequencies cannot be compared in a meaningful way across species or sites or periods unless capture probability is measured (Tobler et al. 2008b, O'Brien 2010*).

According to Caughley (1977) quoted in Williams et al. (2001):

> *An index of abundance or density is any correlative of density.*

The key word is the *correlation* between capture frequency and actual abundance. Usually there is a positive relationship between capture frequencies and abundance or density. At the same time, rarely has it been established that an index measures a constant proportion of the population. As a result, varying detection probabilities could cause mistaken assumptions of contrasts in abundance (Conn et al. 2004). In light of these constraints, we recommend at most comparing within-species within-site frequencies obtained by sampling that has kept camera trap stations, habitats, and sampling space and time constant, and even then exercising caution. With no measure of confidence, and considerable sampling noise, even within species, contrasts must be strong to be considered valid reflections of real contrasts or trends in the system being sampled.

When stations, space, time, habitat are held identical or very similar, strong contrasts such as many stations capturing white-lipped peccaries (*Tayassu pecari*), versus few (for example 75% stations recording white-lipped versus 5% - in a sample area that easily exceeds *T. pecari* home ranges), or marked species composition changes are observed (such as a shift to 45% of camera stations recording collared peccaries in the same area versus 10% previously) are strong suggestions of trend. Similarly, if abundant widely spaced photographs of brocket deer (*Mazama americana*) or pacas (*Cuniculus paca*) are obtained in one such large sample, and not in another, with all or most sampling factors held constant, the suggestion of valid contrast or trend cannot be ignored. Such conclusions do fall into natural history, which has drawn valid conclusions in the absence of alpha levels and confidence intervals for 10,000 years. The take-home point is that when making comparisons, as many aspects of sampling as possible should be held constant, and even then the evaluations of trend should be within species. In the absence of a measure of detection probability, subtle contrasts may well result from sampling and/or natural variation other than abundance.

As with jaguars, individual identification permits much more precise estimation of population density through capture-recapture models. Such identification is possible for some prey species—tapir, giant armadillos, pacas (see Appendix 1 for examples). However, in addition to the difficulties described above, in a survey designed for jaguars, camera spacing may not be appropriate for density estimates for species with smaller ranges than jaguars. For these species, the survey grid may include numerous gaps where individuals of particular prey species have 0 capture probability, therefore violating the assumptions for capture-recapture models (O'Brien 2011, Foster & Harmsen 2012).

One approach to overcome this issue, and take advantage of the logistical outlay in undertaking the jaguar survey, is to utilize inlaid grids simultaneously—either with random placement of cameras within a sub-area of the larger grid or using the same type of locations while spacing cameras closer together within an inlaid grid (Araguillín et al. 2010, Espinosa-Andrade 2012). Because detection probability varies across species, as well as over space and time, Pollock and colleagues (2002) recommend a double sampling approach, including a larger grid to generate the abundance index and a smaller sub-sample to estimate detection probability. If we were to do this more often we could test/validate the inferences about abundances made with capture frequency indices.

An alternative method for estimating relative abundance spatially, rather than strictly numerically, is "patch occupancy" (MacKenzie *et al.* 2002, 2003, MacKenzie & Royle 2005, McShea et al. 2009, Licona et al. 2010, O'Connell & Bailey 2011). Camera trap data on prey species can also be analyzed using occupancy models to evaluate habitat preference within survey areas, relative abundance across wide areas, or species diversity based on observed species and the number of additional species present but not observed (MacKenzie et al. 2006, O'Brien 2008, Tobler et al. 2008a, 2008b). A "naive" patch occupancy index is simply the proportion of camera stations where the target species appears – and by drawing no additional conclusions, interesting inferences about the distribution of prey species can be derived in this way. The software PRESENCE 5.5 (Hines 2012, http://www.mbr-pwrc.usgs.gov/software/presence.html) statistically estimates the proportion of camera stations where the target species is present, according to capture probabilities, even though the species may not be recorded in as many camera stations. Just as CAPTURE uses capture-recapture histories to estimate the total number of individuals present, including un-observed individuals, PRESENCE uses capture-recapture histories in detection based probability models to estimate the total number of camera trap stations where the species is present, including camera stations where the species was not observed. If data are sufficient, complex patch occupancy analyses can incorporate additional variables in order to evaluate habitat preferences or responses to anthropogenic pressures. Sollman et al. (2012) used camera trap based occupancy modeling to examine jaguar and puma correlations with water, roads, and dense habitats. Karanth et al. (2011) examined the influence of prey abundance and human disturbance in field sign based tiger occupancy surveys. The covariates Zeller et al. (2011) examined when analyzing interview based occupancy surveys for jaguar prey included proportions of forest, wetland, water, and distance to edge of protected area.

ADDITIONAL DETAILS ON SURVEY DESIGN AND DATA ANALYSIS

Camera spacing: Dillon & Kelly (2007) found that when camera spacing is large relative to the target species' home range at the site (3 km for ocelots at their site in Belize), then the displacement distances recorded by camera traps are relatively large, possibly reflecting only infrequent long-distance movements or dispersal, and population density may be underestimated. Wegge et al. (2004) found that increasing the trap spacing above 1 km underestimated tiger abundance. However, another study on tigers found that increased trap density simply increased capture probability and the precision of population estimates (Harihar et al. 2009). Obviously spacing can be excessive, with no individuals photographed at more than one camera location, and therefore no displacement information generated at all. At the same time, traps which are spaced too widely may fail to detect individuals if they occupy home ranges that fall between trap locations, violating the assumption of conventional capture-recapture models that the probability of capture of every individual is greater than zero (O'Brien 2011, Foster & Harmsen 2012). Dillon & Kelly suggested that camera spacing should seek to maximize capture probability by including at least 2 stations per average home range, which aligns with Tobler and Powell's (2013) comment that they found the maximum spacing which gave accurate results was about half a home range diameter.

Males vs. females: Camera traps frequently permit confirmation of the sex of photographed animals. However, researchers often do not know what actual sex ratios of target species are in the study site. Therefore they are unable to confirm biases in sex ratios of individuals identified from camera traps, for example if frequent male bias in jaguar surveys (Silver et al. 2004, Maffei et al. 2011a), reflects a real male bias in the landscape. The observed bias may result from methodological issues combined with behavioral differences between the sexes, resulting in lower capture probability for females at the camera trap locations established for the survey. Assuming that females are less detectable than males and move smaller distances (as confirmed for tigers, Karanth et al. 2011b), one solution is to estimate density separately for males and females respectively, rather than pooling all individuals together in a single analysis (Sollman et al. 2011, Tobler et al. 2013).

Behavior: Bridges and Noss (2011) review how camera traps have been used to study a wide range of behavioral topics including nest predation, foraging, circadian rhythms, sociality and niche partitioning, reproduction, and habitat use. Activity and habitat use studies are described further below.

Activity patterns: Camera trap are frequently used to describe activity patterns. The advantage is that they usually monitor multiple locations 24 hours a day for many days or weeks. Independent observations, usually taken to be at least one hour between subsequent photos of the same species at the same camera location, can be grouped by hour or by period of the day in order to describe activity. Individual identification is not necessary, and activity can therefore be described for all species photographed during camera trap surveys (Maffei et al. 2002, Noss et al. 2003, 2004, Trolle 2003, Maffei et al. 2004, 2005, Gómez et al. 2005, Cuéllar et al. 2006, di Bitetti et al. 2006, Grassman et al. 2006, Maffei et al. 2007a, Arispe et al. 2008, Ayala et al. 2010).

Camera trap records of activity are also used to evaluate niche partitioning among sympatric species (de Almeida Jácomo et al. 2004, Maffei et al. 2007b, Kelly & Holub 2008, di Bitetti et al. 2009, Harmsen et al. 2009, Ridout & Linkie 2009, Monroy-Vilchis et al. 2009, di Bitetti et al. 2010, Romero Muñoz et al. 2010), or temporal and spatial relations between predators and prey or relations between wildlife activity and human interventions (Griffiths & van Schaik 1993, Laidlaw & Noordin 1998, Kawanishi & Sunquist 2004, Johnson et al. 2006, Weckel et al. 2006, Ngoprasert et al. 2007, Lucherini et al. 2009, Paviolo et al. 2009, Davis et al. 2011, Harmsen et al. 2011). Aside from time of day, some digital cameras are capable of recording for each photo environmental data such as temperature and relative humidity, factors which may be of interest in particular studies.

Habitat use: A number of studies postulate habitat preferences by comparing camera trap abundance indices across categories of habitats in which camera traps are placed (Trolle 2003, Bowkett et al. 2007, Boas Goulart et al. 2009, Harmsen et al. 2010b, Foster et al. 2010, Davis et al. 2011).

Survival / population turnover: In cases where individuals are identifiable over extended time periods (multiple seasons / years), and camera trap surveys can be repeated, then open population analyses are possible (O'Brien 2011). Karanth and colleagues use camera trap data on tigers in conjunction with open population capture recapture models to estimate key demographic parameters, such as time-specific abundance, annual survival rate, and number of new recruits (Karanth et al. 2006, 2011). Balme and colleagues used camera trap surveys before and after conservation interventions to reduce human-leopard conflicts, finding that annual population growth rate increased significantly (Balme et al. 2009b). Gardner and colleagues provide details of how to formulate and run a series of hierarchical spatial capture–recapture models, and to extend them to demographically open populations, using WinBUGS (Gardner et al. 2010, Royle & Gardner 2011).

Complementary methods for density estimates: Whenever possible, density estimates derived from camera trap surveys should be compared with other available information on the species at the site or at similar sites. For example, researchers have conducted camera trap surveys simultaneously with radio-telemetry in the case of jaguars (Soisalo & Cavalcanti 2006) and ocelots (Maffei & Noss 2008), and with scat DNA in the case of tigers (Gopalaswamy et al 2012) and snow leopards (Janečka et al. 2011). Scat DNA data can be analyzed using the same spatially explicit capture recapture methods described above in order to estimate density. Radio telemetry provides invaluable information for designing appropriate camera trap surveys on ranging behavior and habitat use (for jaguars see Rabinowitz & Nottingham 1986, Núñez et al. 2002, Scognamillo et al. 2003, Cullen et al. 2005, Cavalcanti 2008, Cavalcanti & Gese 2009, Conde et al. 2010).

CHAPTER IV

DENSITY ESTIMATION

The program CAPTURE generates an estimate of abundance, not of density, which researchers have derived by calculating a survey area equivalent to a polygon sampled by the camera traps, buffered by ½ or the full "Mean Maximum Distance Moved" (MMDM), by individuals of the target species during the survey (Wilson & Anderson 1985, Karanth & Nichols 2002, O'Brien 2011). This "effective sample area" (as opposed to the camera trap polygon which is defined by the outer limits of the stations has been necessary to take into account those individuals whose home range was only partly in the polygon, and to avoid estimating population density based on a "cross-roads effect" where jaguar ranges happen to overlap. The buffer has been drawn as a circle around all stations, and the outer limit of that, and also as a set distance around the camera trap station polygon, and the outer limit of that (Silver 2004). Unfortunately, this approach has no theoretical mechanism to link abundance with the survey area in order to estimate density (Williams et al. 2002, Royle et al. 2009a), has been questioned due to the ad hoc nature of estimating the survey area (Efford 2004, Gardner et al. 2009, Royle et al. 2009a, Gopalaswamy et al. 2011) and because it depends directly on the size of the survey area (Maffei *et al*. 2011a, b, Tobler & Powell 2013).

The most severe issue with this approach have been related to small sample areas defining the limits of measurable movement, and thus an underestimate of potential ranges of the cats, and a resulting positive bias and overestimate. Soisalo and Cavalcanti (2006) tested telemetry based density estimates against CAPTURE baed density estimates, finding better agreement with full MMDM. Maffei and Noss (2008), Maffei et al. (2011a, b) recommendations agreed with Soisalo and Calvanti's (2006) conclusions that the full MMDM was less prone to bias results than ½ MMDM and then only when combined with large sample areas that were based on estimations of local home range sizes.

Maffei et al. (2011a) recommended that many of the first generation of density estimates be treated as preliminary until more large sample areas had been tested (e.g. >500km^2), and recommended that future research should emphasize larger survey areas to confirm whether density estimates are consistent when scale of survey is increased. Foster and Harmsen (2012) discussed the issue of effective trapping area (ETA) in detail, clearly stated the circular logic of defining home range/movement lengths by size of area sampled and urged more examination (including simulations) of under what conditions the above described MMDM methods might perform satisfactorily. Since male and female ranges differ greatly in size, Foster and Harmsen (2012) also suggested that gender specific estimates of MMDM might reduce heterogeneity in the data, suggesting separate density estimates. Sollman et al. (2011) and Tobler and Powell (2013) subsequently explored gender specific analyses, with positive results even if dividing already small samples by gender pushed the limits of the SECR models they were using. Meanwhile, preliminary results based on published (Noss et al. 2012) and unpublished data analyzed from several additional sites with the two SECR models introduced in this manual suggest that when using large polygons density estimates generated by Capture are in rough agreement. Using simulated data Tobler & Powell

(2013) suggested full MMDM and their results indicated unbiased results for camera polygon sizes equal to or larger than one male home range.

The frustrations with ad hoc areal estimates CAPTURE requires contributed to development of the spatially explicit capture-recapture (SECR) models which this manual presents.

Box 2: What is R?

R is a language and environment for statistical computing and graphics. R provides a wide variety of statistical (linear and nonlinear modeling, classical statistical tests, time-series analysis, classification, clustering, etc.) and graphical techniques, and is highly extensible. The S language is often the vehicle of choice for research in statistical methodology, and R provides an Open Source route to participation in that activity.

R is an integrated suite of software facilities for data manipulation, calculation and graphical display (Venabales & Smith 2009, Adler 2010). It includes

- an effective data handling and storage facility
- a suite of operators for calculations on arrays, in particular matrices
- a large, coherent, integrated collection of intermediate tools for data analysis
- graphical facilities for data analysis and display either on-screen or on hardcopy
- a well-developed, simple and effective programming language which includes conditionals, loops, user-defined recursive functions and input and output facilities

The term "environment" is intended to characterize it as a fully planned and coherent system, rather than an incremental accretion of very specific and inflexible tools, as is frequently the case with other data analysis software.

R, like S, is designed around a true computer language, and it allows users to add additional functionality by defining new functions. Much of the system is itself written in the R dialect of S, which makes it easy for users to follow the algorithmic choices made. For computationally-intensive tasks, C, C++ and Fortran code can be linked and called at run time. Advanced users can write C code to manipulate R objects directly.

Many users think of R as a statistics system. We prefer to think of it of an environment within which statistical techniques are implemented. R can be extended (easily) via packages. There are about eight packages supplied with the R distribution and many more are available through the CRAN family of Internet sites covering a very wide range of modern statistics, **including SPACECAP and secr**.

Recent advances in spatially explicit capture recapture (SECR) have resulted in a new approach that directly estimates animal density by using information on capture histories in combination with the location of the individual capture under either a Bayesian or likelihood analysis framework (Borchers & Efford 2008, Royle & Young 2008, Gardner et al. 2009, Royle *et al*. 2009a, Royle & Gardner 2011). See Appendix 2 for an explanation of some of the above terminology as it relates to the two population estimation models which are presented in subsequent sections of this text.

DENSITY

Key assumptions of the SECR models are that animals occupy home ranges, home ranges are circular and are dispersed randomly, and successive trapping occasions are independent. The probability of capture is a declining function of distance between the range centers and camera traps, directly analogous to a detection function in distance sampling (Efford 2004, Royle et al. 2009a). Efford and collaborators (2004, 2009) offer the software package DENSITY (http://www.otago.ac.nz/density) which operates in a Windows interface, requiring two input files: trap layout (numbered location) and capture data (i.e., numerical designations for sampling session, animal identification, trap day, and trap location). Additional information required includes trap layout type, and a buffer value recommended to be several times the estimated home range diameter for the target species which establishes for the analysis a state space area that encompasses the survey area but extends well beyond it on all sides.

→ See Appendix 3 for tips on how to enter the data into the program.

Currently two packages for running SECR models in the programming language R (see Box 2) are available: an R version of DENSITY called secr, and SPACECAP. While these programs have complete manuals the following text also works through some examples.

SECR FOR R

The R package secr, developed by Efford and colleagues (2009, http://www.otago.ac.nz/density) utilizes the likelihood approach to SECR models. Efford (2010) provides a detailed manual. Once you have uploaded the secr package to R on your computer, you run the analysis using R scripts (see Box 3 for an example), as well as the same two input files described for DENSITY above, the trap layout type (proximity in all cases, because animals are recorded but not captured), and a buffer value recommended to be five times the estimated home range diameter for the target species. For example, analyses from Kaa Iya National Park in Bolivia utilized a buffer of 15,000 m in the case of jaguars and pumas; and 6,000 m in the case of ocelots and tapirs. Researchers specified the null model, with a half-normal detection function, and a binomial or Bernoulli encounter process. The secr package automatically creates a mesh for the analysis based on the trap array and the buffer size, unless the user creates his/her own 'mask'. For this analysis, we used the default mesh which was generally between 0.5 and 1 km in spacing (Noss et al. 2012).

A half-normal model describes the probability of capture (P) as a function of distance (d) from home range center to trap, in the absence of competition. $P_{ij} = g_0 \exp(-d_{ij}^2/(2\sigma^2))$, where g_0 is the probability of capture when the trap is located exactly at the center of the home range, and σ is a measure of home range size (Buckland et al. 1993, Efford 2004). One model that is most relevant to camera trapping studies is the Bernoulli or binomial encounter model. Under this model, an individual can be caught at most one time in any single trap, but in each of an arbitrary number of traps during any particular trapping interval. Although individuals can visit a camera station an arbitrary number of times during any sampling interval, multiple visits during a single short occasion (e.g., a night) are not likely to be independent and thus may contribute relatively little information. Camera trapping studies generally consider a trapping interval to be a 24-hour period. Each trap can also catch multiple individuals (Royle & Gardner 2009).

Box 3: R script for secr, unconditional likelihood model*, jaguars in Cerro 2002 camera trap survey.*

```
library(secr)
capthist<-read.capthist('C:\\secr\\Cerro2002Jaguaresdensidad.txt',
'C:\\secr\\Cerro2002y2003Ubicaciones.txt',
detector='proximity',fmt='trapID', noccasions=60)
buffer=15000
secr.0 <- secr.fit (capthist , model = g0 ~ 1, trace = FALSE,
buffer=buffer)
secr.0
```

> *The half-normal model of intrinsic trappability was initially described by Calhoun and Casby (1958), and has much in common with detection models used in analyzing distance data and trapping webs (Buckland et al. 1993, Link and Barker 1994, Borchers et al. 2002). The fundamental assumption of distance analysis is that individuals located exactly on a transect or at a detection device are recorded with certainty (g_{0}=1). See Appendix 2 for a brief description of detection functions.*
>
> *It is a fundamental assumption of the method that animals occupy home ranges (in mathematical terms, capture locations are drawn at random from a stationary distribution). The method cannot be assumed to work where a high proportion of individuals are nomadic or transient, and its robustness in these circumstances has yet to be investigated.*
>
> *The weakest aspect of the new method is probably the assumption that đ, the observed mean distance between successive captures of an individual, provides reliable information on σ, the spatial scale of the detection function. This assumption is justified when successive trapping occasions are independent…. Other breaches of assumptions appear more likely to affect the precision of estimates than to cause significant bias. Non-circular ranges, clumped dispersion of individuals, and individual variation in g0 and s, are all likely to affect the variance of density estimates by the present method (Efford 2004).*

Box 4 gives an example of a secr output file. The results include the fitted real parameters together with their standard error (SE), lower and upper 95% confidence limits (lcl, hcl):

- D is the density estimate (1.464315e-04 individuals / ha or 1.46 individuals / 100 km^2)
- g0 is the capture probability (5.209954e-03 or 0.005)
- sigma is the measure of home range size (4,104 m)

```
Box 4: secr output (from example in Box 3 above).

Fitted (real) parameters evaluated at base levels of covariates
link      estimate  SE.estimate          lcl           ucl
D        log 1.464315e-04 8.536679e-05 5.072496e-05 4.227148e-04
g0     logit 5.209954e-03 1.974809e-03 2.475666e-03 1.093107e-02
sigma    log 4.104624e+03 1.110821e+03 2.437663e+03 6.911512e+03
```

→ See Appendix 4 for tips on how enter the data to the program.

SPACECAP

The R package SPACECAP applies the Bayesian approach, specifying the same model as was carried out in the R package secr, using Markov-chain Monte Carlo (MCMC) to simulates draws of each home range center from the posterior distribution (Gardner et al. 2009, Gopalaswamy et al. 2012b, Repucci et al. 2011, Royle et al. 2009a, 2009b). The software package is available at http://cran.r-project.org/, and Gopalaswamy and colleagues (2011) provide a detailed manual (see also Appendix 2 for further details on Bayesian models and terminology). Upon running the package in R, SPACECAP opens a Windows interface. Three input files are required (the first two similar to those used in DENSITY and secr): animal capture details (information on animal identification, trap location, and sampling occasion), trap deployment details (spatial location, dates when specific traps were active, sampling occasion designation), and state-space details (a mesh of equally spaced points covering the trap area and an extended area surrounding it, representing potential animal activity centers). In Kaa Iya analyses, estimates of the state-space include the camera polygon and a buffer of 15,000 m for jaguars and pumas, and 6,000 for ocelots and tapirs. For animals with relatively large home ranges—jaguars and pumas—the mesh size was set to 1 km apart (a 1 km^2 pixel), whereas for the other two species the mesh size was set to 0.5 km apart (a 0.25 km^2 pixel). Thus the state-space input file for each survey and species is a grid of points spaced 1 or 0.5 km apart, respectively, for the buffered area including the camera polygon. These values are estimates based on observed movements and overlap of individual ranges determined by camera trap surveys; in the case of ocelots and tapirs radio telemetry results from the region suggested the estimates (Noss et al. 2012).

For all analyses researchers used the following recommended model definitions: trap response absent, spatial capture-recapture, half-normal detection function, and Bernoulli or binomial encounter model. The following SPACECAP settings were maintained as recommended by the program developers: 50,000 iterations, 10,000 initial burn-in values, thinning rate of 1, and data augmentation of 5-50 times the number of animals photo-captured in each survey. This last parameter varied by species and survey: in the Kaa Iya cases from 25 for jaguars (a minimum of 5 individual jaguars identified in a single survey) to 500 for ocelots and tapirs (a maximum of 69 individual ocelots identified in a single survey).

The 95% upper bound of the Nsuper estimate should exceed the data augmentation value: for example the value of 24 in Box 5 below is barely less than the augmentation value of 25 for jaguars, and the analysis should be run again with a higher augmentation value. SPACECAP developers recommend a minimum of 50,000 iterations, and we have not used higher values because of the time required to run the analyses—a minimum of 4 hours in the case of jaguars with relatively few captures and recaptures, and over 50 hours in other cases. The burn-in value may be altered if users wish to increase the number of initial iterations to be discarded as potential outliers that are used to determine the final results. The thinning rate indicates the number of iterations that are stored during the analysis. A thinning rate of 1 stores all iterations, while a rate of 2 stores only every 2^{nd} iteration.

Box 5: SPACECAP output (jaguars, Cerro 2002 survey)

	Posterior Mean	**Posterior SD**	**95% Lower HPD Level**	**95% Upper HPD Level**
sigma	2.4441	1.304	0.7412	4.9809
lam0	0.0097	0.0046	0.0039	0.0179
beta	-1.1253	4.2674	-9.1117	5.922
psi	0.4138	0.1904	0.1017	0.8122
Nsuper	12.241	5.5157	5	24
Density	**0.6429**	0.2897	0.2626	1.2605

In Box 5 above, SPACECAP presents the results (posterior mean, posterior standard deviation, and 95% confidence limits) for the model parameters:

- sigma may be viewed as a "range parameter" of an animal, and must be converted to meters using the following formula: +SQRT(sigma/2)*5*1000. Sigma = 2.4441 = 5527 m.
- lam0 = 0.0097 is the expected encounter rate of an individual "i" in trap location "j" at sampling occasion "k", whose home-range centre is exactly at the trap location. We can convert Lam0 to a capture probability by using 1-exp(-Lam0), which is essentially equal to Lam0 when detection is very low.
- beta is the regression coefficient that measures the behavioral response, relevant if the user selects the "trap response present" alternative when selecting the model definition to run SPACECAP.
- psi is the ratio of the number of animals actually present within S to the maximum allowable number (set by the user during data augmentation).
- Nsuper is the population size of individuals – the number of activity centers located in the state space S.
- Density is equivalent to Nsuper / S where S is the area of the state-space, and is reported directly as 0.6429 individuals / 100 km^2.

*A heuristic description of **data augmentation** is that it arises by simply adding excess 'all zero' encounter histories to the data set. That is, for M sufficiently large, then we can augment the data set with M − n all-zero encounter histories we then recognize that the resulting model for the augmented data is a zero-inflated version of the model for the complete data set (i.e. as if N were known). In models with individual effects, data augmentation is a convenient framework because it allows us to retain a maximal set of random effects in the (augmented) data set, and their values are updated at each iteration of the MCMC algorithm (Royle et al. 2009a).*

SPACECAP also reports a file to generate a surface density map (called pixeldensities_val_<timestamp>.csv). This table reports estimates of pixel densities, and the corresponding X_COORD and Y_COORD of the pixels. The table can be then imported into any GIS platform to view the pixel surface densities (Gopalaswamy et al. 2011).

Added to SPACECAP in 2011 are two statistics with which users can evaluate the results. SPACECAP assesses the convergence of the MCMC run by using the Geweke (1992) diagnostic statistic which is estimated for all the estimated parameters. This statistic produces the z-score values so that a value of |z-score|>1.6 will imply that the MCMC analysis has not been run long enough. SPACECAP also assesses the adequacy of a model using the Bayesian P-value, as implemented in Royle et al. (2011b) so that any value that is close to 0 or 1 would imply that the model is inadequate (Gopalaswamy et al. 2011).

→ See Appendix 5 for tips on how to enter the data into the program.

CONSIDERATIONS ABOUT DENSITY ESTIMATION PROGRAMS

Researchers are testing approaches to estimate density for species where individual identification from camera trap photos is not possible (Rovero & Marshall 2009). New camera trapping techniques are developing that use random camera placement, combined with information on species' day range, to address spatial variability (Rowcliffe et al. 2008, 2011). However, random placement is unrealistic for most jaguar field studies because capture probabilities would be impossibly low. Given that capture probability is already low even in studies that target jaguars (~2 per 100 trap nights), the increased effort required to obtain captures using random placement is probably not realistic. The conventional study approach for jaguars – semi-systematic, nearly regularly-spaced, traps set to target jaguars (i.e., on roads, trails, games trails, riverbeds, etc.) – violates the random placement of traps which has proven to be necessary to generate unbiased estimates in the gas model approach of Rowcliffe et al. (2008).

Based on our published and unpublished analyses, we recommend using SPACECAP or secr rather than the program Capture using the MMDM approach, irrespective of grid size. Other researchers who have recently compared density estimation methods also recommend SCR models to avoid over-estimation of population density and potentially inappropriate management actions as well as facilitating comparisons across sites and species and over time (Obbard et al., 2010; Gerber et al., 2012). Each of the two SCR models evaluated in this paper offer distinct features that can be of benefit to practitioners. The maximum likelihood approach is faster in terms of computation times (minutes instead of hours or days with current computers) and does not require much user specification or evaluation of the model output (Efford, 2011). In fact, the secr package will provide a warning if the buffer size does not appear large enough. On the other hand, the Bayesian approach may be more appropriate for small sample sizes, typical when sampling rare or elusive species (Kéry et al. 2010).

However, the user must also be very careful with the mechanics of the analysis, including the influence of the priors (ensuring that data augmentation and the state space area are sufficiently large), and that the MCMC chains have reached the stable distribution. Posterior distributions of the parameters should always be checked against the priors and against the distribution of the parameter iterations. Insufficient data augmentation will truncate the abundance estimate, whereas a state space area that is too small will generate an over-estimate of density.

In addition to the summary results (Box 5 above) which allow you to confirm whether data augmentation was larger than Nsuper, SPACECAP provides the full list of MCMC outcomes for the 50,000 iterations if that is how many you run. Therefore you can confirm whether the values of the variables have stabilized in the final iterations, or whether you need to run still more iterations. The state space may be too small, but cannot be too large. Therefore you may want to test whether increasing the state space alters the density estimate, to ensure that a further increase in the state space area is not necessary. Given the time that SPACECAP takes to run, it is preferable to run these tests in secr or DENSITY.

Some of the Kaa Iya field surveys have generated too few captures and recaptures for spatially explicit models to estimate the full set of parameters. With wide-ranging species at low population densities, this limitation can only be addressed by expanding the survey area and lengthening the survey period. In such cases, it also makes sense to consider a SECR model that allows for demographically open populations (Gardner et al., 2010).

Average jaguar and puma ranges in the Chaco exceeded camera trap polygons for nearly all of the first generation surveys in the Kaa-Iya landscape in Bolivia. In the largest survey, a jaguar photographed in previous years crossed the entire camera trap polygon (434km²), a straight-line distance of 34 km (Romero-Muñoz et al., 2007) which: 1) is argument for the limitations of the MMDM approach: and 2) argument for using spatially explicit programs which handle the space issue slightly better. The spatially explicit programs assume that jaguar home ranges are roughly circular in shape when they actually may be elliptical, or irregular polygons based on the distribution of food resources. Despite this caution, these programs represent an advance over the ad hoc estimates of sampling area involved in all but the largest polygons using Capture and MMDM. Additional telemetry information can help guide survey design as suggested by Soisalo and Cavalcanti (2006) and Maffei & Noss (2008) yet is not always available. Telemetry based home ranges vary even among individuals within study areas and thus represent rough guidelines, Appendix B in Tobler & Powell (2013) provides a useful compendium. Unless local, home ranges, do become another form of guesswork, they are a best guess input even in spatially explicit models. All of this ambiguity seems best compensated for by the general mantra "go big".

Although SPACECAP and secr are less sensitive than the CAPTURE / MMDM approach to grid size, we recommend camera polygons several times larger than average home range (known or estimated) of the target species. For jaguars in South America, this implies camera grids extending over 200-300 km^2 or even much more. Though we have recommended minimal sample areas in Mesoamerica, this lower end is guided by a more limited set of home range data than currently available from South America, and may become outdated. For either region and for any models, larger sample areas will avoid multiple issues than can result in inaccurate estimates.

The array must be dense enough to ensure multiple camera traps per animal home range, and thereby increase the likelihood of detecting individual animals present and of acquiring multiple recaptures of each individual (O'Brien 2011). None of the density estimation models can generate precise results with few individuals captured and few recaptures. Both SCR models failed to generate density estimates in Kaa-Iya surveys where individuals photographed were few (4-6 or fewer jaguars, pumas, tapirs, giant armadillos), where captures + recaptures were few (9-20 for jaguars, pumas, ocelots, tapir, giant armadillos), and/or where individuals were rarely photographed at more than one location (Geoffroy's cats, tapirs).

Camera spacing designed for wide-ranging species (jaguar, puma) will not be appropriate for species with smaller ranges (ocelot, Geoffroy's cat, tapir, giant armadillo). A survey targeting multiple species should therefore include arrays with tight spacing for the latter species within a larger array with wide spacing for the former. Adequate sampling effort rather than convenience or resource limitations must guide study design.

FUTURE DIRECTIONS AND MONITORING

We concur with Foster and Harmsen's (2012) recommendation for simulation studies to guide study design and evaluate the performance of SCR estimators prior to implementing field work. Females use different size areas than males, thus can have different home range parameters, possibly pack at different densities, and may even have subtle contrasts in habitat selection. Sollmann et al. (2011) used sex-specific spatial models to estimate density while examining sex-specific encounter rates and movement parameters. However, even with 119 camera trap stations distributed across 1320km² splitting jaguar numbers by gender resulted in small sample sizes in their particularly low density study area. Tobler and Powell (2013) recommend all jaguar densities studies include sex covariates for the base encounter rate at activity center, and distance parameter related to home range. They also suggested "borrowing" home range sizes and encounter rates from multiple surveys in the same area, as sharing the parameters across surveys can help rigor, and parameters estimated from larger survey areas can be used to correct for polygon size bias in smaller areas, which they did for areas in Peru (Tobler et al. 2013). Conducting multiple surveys in an area will not only help validate results and detect errors; the history developed will enhance ecological insights and inform conservation actions.

Monitoring requires that trends observed are meaningful on a biological level and across the time intervals of interest. The abundant challenges in generating accurate estimates described in this document, in Harmsen and Foster (2011), Maffei at el (2011), and Tobler and Powell (2013) testify to the high potential of sampling based variance, to which we might add seasonal based variance. De la Torre and Medellín (2011) obtained nearly identical density estimates for two dry seasons in the Lacandona Forest of Mexico, but a different density during the wet season. When trend is a goal, an expanded version of maxims of constant proportion sampling (Lancia et al. 1994) applies. Keep a number of factors constant when attempting to detect trends. Stay in one place and vary as few sampling parameters as possible. Appendix 6 presents a brief discussion of some software to estimate statistical power in detecting trends.

This manual and appendices provide initial guidance for using spatially explicit models. WCS jaguar efforts focus on very large jaguar landscapes with generally challenging access. With limited financial and human resources and equipment to monitor huge poor access areas, density estimates are infeasible as the sole tool for monitoring jaguar populations. Presence-absence based occupancy analyses use detection histories much as capture-recapture models use marked animals, focus more on space than numbers, and offer a way to cover more ground, in a lighter weight and more sustainable way (MacKenzie et al 2006). Where substrates and access allow, field sign based occupancy modeling (Karanth et al 2011c, Hines et al. 2010) has exciting potential. Where local guards and cooperators allow, interview data also has high potential with pilot results presented in Zeller et al. (2011). If these can be combined in innovative ways, low budget interviews and sign patrols can complement intensive density focused monitoring, covering more ground in a cost effective manner to measure the success of our conservation interventions.

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APPENDIX 1

Individual identification

Identification of individual animals with spots or stripes (in the Kaa-Iya landscape jaguars *Panthera onca*, ocelots *Leopardus pardalis*, Geoffroy's cats *L. geoffroyi*, margays *L. wiedii*, and pacas *Cuniculus paca*) is straightforward, particularly when paired camera traps obtain photos of both flanks simultaneously (Arispe 2007). Tail spots and rings (number, width, full or partial rings) also facilitate identification in the case of the same cats and raccoons *Procyon cancrivorus* (Arispe et al. 2008).

Figure A1.1: Two different ocelots.

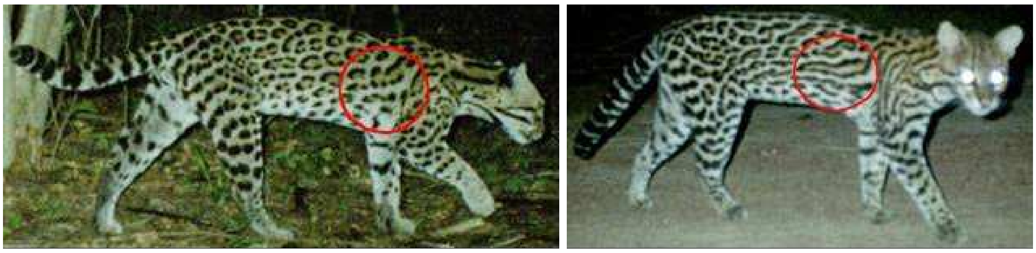


Figure A1.2: Two different pacas.

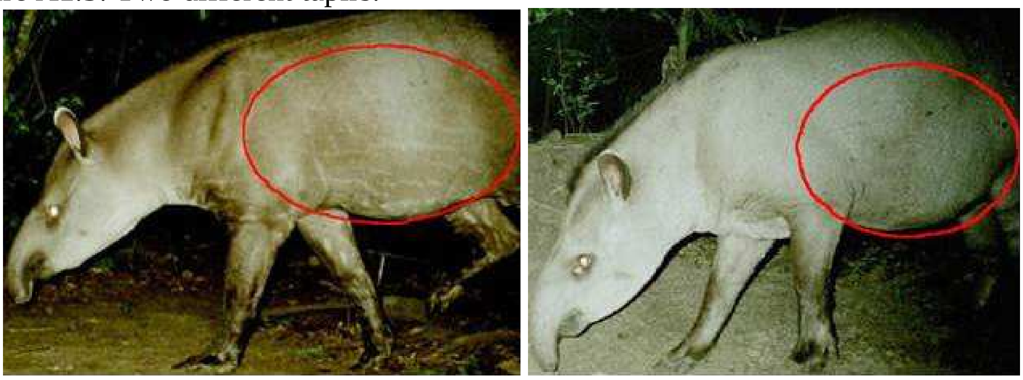
Figure A1.3: Two different raccoons.

Puma *puma concolor*: Adult pumas can be identified by obvious marks—kinked tails, size and shape of black tail tip, black muzzle markings, scars, ear nicks; by less obvious marks—scars that healed over time [e.g. from botflies]; and by subtle marks—undercoat spot patterns, coloration on the underside of legs, tail carriage, and body shape and carriage (Kelly et al. 2008, Paviolo et al. 2009, Mazzolli 2010, Negrões et al. 2010, Soria-Díaz et al. 2010).

Figure A1.4: Two different pumas.

Tapir *Tapirus terrestris*: A number of unique features serve to distinguish individuals: scars, white spots and stripes on the stomach or legs, black spots on the face or sides, white markings at the base and fringe of the ears, torn or missing ears, toenail markings or color, tail length and white markings on the tail. Coat color and body structure vary as well among individuals, and sex can often be determined from the photographs (Holden et al. 2003, Noss et al. 2003, Montenegro 1999).

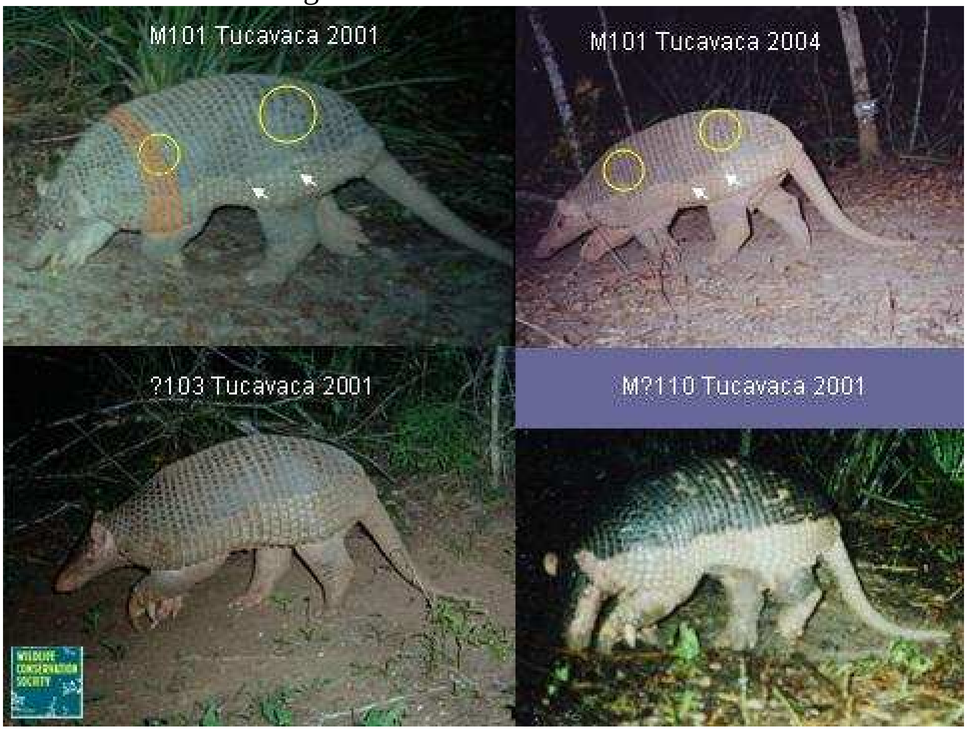
Figure A1.5: Two different tapirs.



In the case of pumas and tapirs, researchers should take care not to use temporary markings as identifiers, for example marks from mud or shallow scratches which could disappear during the two-month survey period. They should also account for the differences in the observed features resulting from differences in camera angle, body position, and lighting conditions (Kelly et al. 2008, Noss et al. 2003, Oliveira-Santos et al. 2010).

Giant armadillo *Priodontes maximus*: The unique scale patterns permits the identification of individual animals, while the genitalia are infrequently shown and do not permit sexing every individual. The dividing line between dark and light scales on the carapace and on the hind legs is particularly noteworthy, as is the number of light scales per row from the lower edge of the carapace up to the dividing line (Figure 9) (Noss et al. 2004).

Figure A1.6: Identification of giant armadillos at Tucavaca.



Some authors have questioned the identification of subtly-marked individuals from camera traps (Oliveira-Santos et al. 2010), especially when using temporally variable traits such as scars (Foster & Harmsen 2012, Goswami et al. 2012). Researchers should generally present density estimates in these cases as tentative, for example based on the minimum number of individuals detected, as determined by the most conservative identification of the most distinct individuals. Misidentification errors can also be modeled into capture-recapture analyses (Link et al 2010, Yoshizaki et al. 2009). We concur that the use of temporary and ephemeral markings has constraints, particularly for long term studies. At minimum, when used with care, the individuals identified provide valuable information about the jaguar's prey and competitors in the study area.

APPENDIX 2

Terminology related to model development and testing

Detection function: In Distance sampling and analysis this is a function which models the declining probability of encountering an animal with increasing distance from either a line transect, or a point from which animals are observed in 360º. The shape of the scatter of observation data may have various forms as it declines from probability of encounter 1 at line or center, and declining with increasing distance away. There are some very indirect homologues between detection functions in Distance sampling and how encounters with increasing distance from the center of the home range are handled in the Capture-Recapture program Density. The probability of an observer seeing an animal on a line transect or at the center point is 1, and this detection probability declines at increasing distance away according to a function that is defined by variables such as species, habitat, local behavior, etc.. In Density declining probabilities are expected with increasing distance from the centroid. However, a jaguar does not necessarily occupy with greater frequency the center of its home range; it may in fact spend more time at various points close to the periphery. At the same time, camera trap stations constitute multiple observers in space. Thus end the similarities between Distance sampling detection functions and the calculations involved in Density but the consideration of detection functions can be helpful in understanding how Density handles space.

Likelihood Ratio Tests are a tool to assess the adequacy of models in characterizing data and comparing models which differ in their parametric structure. These model comparisons are structured as a hypothesis test. The null hypothesis is that the hypothesized model fits the data as well as the alternative model, and the alternative hypothesis is that the alternative model fits the data better than an alternative model. Typically the alternative model is more general than the null, so tests relate to relaxation of parameter restrictions and the sequence begins with goodness of fit tests for a general model. The likelihood ratio tests are made with the assumption that a more general model will fit the data. In contrast, **Maximum Likelihood** is used to develop and refine models and requires knowledge of the underlying distribution of a random sample and actual sample values. One presumes to know the mathematic form of the distribution function, but not the values which, with the function, define the distribution. One estimates that value by sampling the population, and using the distribution function as a "likelihood" function. A value is chosen to maximize the function which is "parameterized" by sample values. The sample values play a role in defining the function values, with the goal of generating a model which best fits the data. The calculations can be somewhat complex, with notations for functions, derivatives of logarithms, and estimates of probability, but maximizing a likelihood function involves choosing an estimate for each parameter which defines the probability distribution which best fits the data (Williams et al. 2002).

The Maximum Likelihood Framework utilizes the number of animals captured and their capture histories, including the spatial distribution of those captures, to estimate the parameters of a capture function and the parameters of a spatial point process governing animal density and distribution. The framework assumes that home-range centers occur *independently in a plane according to an inhomogeneous Poisson process, and that captures between animals are also independent. In turn, the model estimates the probability of observing each individual's capture history given the fact that it was captured, the conditional density of home-range centers, and the maximum likelihood estimate of the density surface and number of animals in the area (Borchers & Efford 2008).*

Akaike Information Criteria (AIC) are used to test the relative fit among alternative models (Buckland et al. 1993). Model selection takes place under an optimization framework rather than hypothesis testing. The details are described in Buckland et al. (1993). The AIC balances the fit of a model to the data against additional parameters using the principle of parsimony. In its formula, a measure of likelihood for the model is balanced with a penalty term for the number of parameters in the model. In other words, the best fitting model with the least number of additional parameters is selected. While Goodness of Fit statistics are useful measures of a model, the AIC can provide more agility in assessing its utility (Williams et al. 2002).

Bayesian Statistical Methods seek to provide a probabilistic characterization of uncertainty about parameters based on the specific data on hand. These methods which require considerable iterations have become more popular in recent years due to faster computers and more efficient methods for solving complex Bayesian inference problems. In the Bayesian view, as in the classical views of statistics, data are realizations of random variables, but in the Bayesian view the parameters of the model are also random variables. With both data and parameters viewed as random variables according to the calculation known as Bayes' Rule, a probability distribution is generated based on the data, which is referred to as the posterior distribution. In other words the Bayesian processes form inferences based on the posterior distribution, conditional upon observed data (MacKenzie et al. 2006).

In general terms, the prior distributions of parameters inform the posterior distribution, which is the basis of Bayesian inference. Expert opinions can inform "priors" resulting in strong prior distributions, leading to less uncertainty in posterior distributions.
A likelihood approach uses available data to determine the ration of likelihood functions, with each evaluated at parameter values, maximizing respective likelihood (Williams et al. 2002). The Bayesian approach uses the sequential collection of data to specify transitions from prior probabilities to posterior probabilities. This is an iterative process, which can be time consuming, during which the posterior probabilities resulting from data collection in one period become the prior probabilities for the next period.

The Bayesian Framework likewise supposes that each individual in the population has a center of activity, or home range center, about which the animal's movements are distributed randomly according to some probability rule; and that these home range centers are distributed uniformly. Due to movement, some individuals captured have a home range center that is located outside of the physical area that was sampled. The framework specifies a point process model that governs the distribution of the home range centers, and adopts a Bayesian approach to analysis of the model based on Markov chain Monte Carlo (MCMC) which simulates draws of each home range center from the posterior *distribution. In practice, we do not observe the individual centers, nor do we observe a complete set of locations for each individual due to imperfect sampling of individuals. Given the observation model, the framework devises the joint probability distribution of the observations and underlying process (the locations of the individuals), and thereby estimates the number of individual activity centers located within the sample unit. The model augments observed data set with a large number of ''all zero'' encounter histories. The augmented zeros correspond to ''pseudo-individuals,'' only a subset of which are members of the population that was exposed to sampling. The model in turn determines the probability that an individual on the list of pseudo-individuals is a member of the sampled population, estimates the individual activity centers, and the absolute density of home range centres in the region containing the trap array. MCMC methods obtain a sample of the model parameters from the posterior distribution by Monte Carlo simulation. Typically, a large sample of dependent draws from the posterior is obtained after an initial sample (referred to as the ''burn-in'') is discarded to ensure that subsequent draws are being generated from the target distribution. Within the MCMC framework, the individual activity centers are regarded as missing observations, and they are estimated by Monte Carlo sampling from the posterior distribution (Royle & Young 2008, Royle et al. 2009a).*

Monte Carlo and Boot Strapping simulation methods are computer-intensive re-sampling of data used to obtain estimates of the bias and precision in population estimates.

Details of the maximum likelihood and Bayesian processes entailed in Density, secr R and Spacecap follow.

Maximum Likelihood Framework:

The likelihood, or equivalently here, the joint distribution of the number of animals captured n, and their capture histories $\omega_1, \ldots, \omega_n$ can be written in terms of the marginal distribution of n and the conditional distribution of $\omega_1, \ldots, \omega_n$, given n, as

$$L(\Phi, \theta \mid n, \omega_1, \ldots, \omega_n) = Pr(n \mid \Phi, \theta) Pr(\omega_1, \ldots, \omega_n \mid n, \theta, \Phi) \qquad (1)$$

where θ is the vector of capture function parameters and Φ is a vector of parameters of the spatial point process governing animal density and distribution. We expand on the forms of $Pr(n \mid \Phi; \theta)$ and $Pr(\omega_1, \ldots, \omega_n \mid n; \theta; \Phi)$ below.

Suppose home-range centers occur independently in a plane according to an inhomogeneous Poisson process with rate parameter $D(X; \Phi)$, with associated parameter vector Φ. Then assuming independent captures between animals, the marginal for n is Poisson with rate parameter $\lambda(\Phi; \theta)$ that arises from integrating the Poisson process with the probability of being caught at least once: $\lambda(\Phi, \theta) = \int_{R2} D(X, \Phi) p.(X, \theta) dX$.

To enhance readability, we sometimes omit the parameter vectors as arguments in our development below. Assuming independent captures between captured animals, the conditional distribution for $\omega_1, \dots, \omega_n$*, given n is* $Pr(\omega_1, \dots, \omega_n \mid n, \Phi, \theta) \equiv Pr(\omega_1, \dots, \omega_n \mid \omega_{1.} > 0, \dots, \omega_{n.} > 0; \Phi; \theta) = \prod^{n}_{i=1} Pr(\omega_1 \mid \omega_{1.} > 0, \Phi, \theta)$*, where* $Pr\ \omega_1 \mid \omega_{1.} > 0, \Phi, \theta) = \int_{R2} Pr(\omega_1 \mid \omega_{1.} > 0, \Phi, \theta) f(X \mid \omega_{1.} > 0, \Phi, \theta) dX$ *is the probability of observing capture history* ω_1 *for individual i, given that it was captured.*

We can express each of the terms inside the integral in terms of the capture probability function $p_{ks}(X, \theta)$ *and inhomogeneous Poisson process rate* $D(X, \Phi)$*. The probability of observing capture history* ω_1 *for individual i, given that its home-range center is at X, and that it was captured, is* $Pr(\omega_1 \mid \omega_{1.} > 0, X) = p.(X)^{-1} \prod^{S}_{s=1} \prod^{K}_{k=1} p_{ks}(X)^{\delta k(\omega 1s)} [1 - p_{.s}(X)]^{1-\delta.(\omega 1s)}$*, (omitting* θ *for readability) where* $\delta k(\omega_{1s}) = 1$ *if* $\omega_{1s} = k$ *and is zero otherwise,* $\delta.(\omega_{1s}) = 1$ *if* $\delta k(\omega_{1s}) > 0$ *for any* $k = 1, \dots, K$ *and is zero otherwise. Assuming independence of capture between occasions,* $p.(X) = 1 - \prod^{S}_{s=1} [1 - p_{.s}(X)]$*.*

The second term in the integral, the conditional density of home-range centers given an animal is captured, can be expressed as follows:

$$f(X \mid \omega_{1.} > 0, \Phi, \theta) = \frac{D(\boldsymbol{X}; \boldsymbol{\phi}) p.(\boldsymbol{X}; \boldsymbol{\theta})}{\int_{\mathcal{R}^2} D(\boldsymbol{X}; \boldsymbol{\phi}) p.(\boldsymbol{X}; \boldsymbol{\theta})\, d\boldsymbol{X}} = \frac{D(\boldsymbol{X}; \boldsymbol{\phi}) p.(\boldsymbol{X}; \boldsymbol{\theta})}{\lambda(\boldsymbol{\phi}, \boldsymbol{\theta})}$$

The model parameters θ *and* Φ *can be estimated by maximizing the likelihood Equation (1) with respect to them. Evaluating* $D(X; \Phi)$ *at the maximum likelihood estimate (MLE)* Φ*-hat provides an estimate of the density surface. The mean value of* $D(X; \Phi\text{-hat})$ *over an area is the MLE of the mean animal density in the area, and the MLE of number of animals in the area is the integral N-hat = R* $D(X; \Phi\text{-hat})dX$*. (Borchers & Efford 2008).*

Bayesian Framework:
Suppose that each individual in the population has a center of activity, or home range center…. The home range center for individual i is the point si = (s_{1i}, s_{2i})*, about which the movements of animal i are distributed (in a manner to be described precisely) according to some probability rule. Thus, si ; i = 1, 2, ... , N represent the home range centers for all individuals in the population, which will be defined to be those individuals within some large region S that contains the sample unit as a strict subset. The sample unit* (camera trap grid in our case*) will be denoted by the set D S. We will assume that* $\subset$ *the* s_i *are uniformly distributed over S. In practice, we will prescribe S (e.g., by specifying coordinates of some polygon that contains the sample unit)…. The model postulates, due to movement, that there are individuals captured having an* s_i *that is located outside of the physical area that was sampled. The model therefore implies the existence of some S, and we must choose it to be sufficiently large so that it does not influence the parameter estimates. More practically, we specify the model in terms of a point process model that governs the distribution of the points* s_i*, and we adopt a Bayesian approach to analysis of the model based on Markov chain Monte Carlo which requires that we simulate draws of each* s_i *from the posterior distribution. We must therefore describe, explicitly, the region within which those* s_i *are simulated, and that region is S. Essentially, S is a prior distribution on the potential location of captureable individuals.*
We suppose that an individual moves around randomly according to some probability distribution function, $g(s; \theta)$*. We will denote the coordinates at sample times t as* $u_{it} = (u_{1,it}, u_{2,it})$ *to distinguish them from the individual centers…. In practice, we do not*

observe the individual centers, s_i, nor do we observe a complete set of ($u_{1,it}$, $u_{2,it}$) pairs for each individual due to imperfect sampling of individuals.

Given the observation model, we will devise the joint probability distribution of the observations and underlying process (the locations of the individuals), and this will enable us to estimate the number of individual activity centers located within the sample unit, or in any, arbitrary region of S.

The model is a specialized case of the individual covariate models, wherein the individual effect is latent (i.e., unobserved)…the location of individuals at each sample occasion are realizations of a partially observed random variable, and they must be removed from the conditional likelihood by integration. Alternatively, Bayesian analysis can be accomplished very directly using methods of Markov chain Monte Carlo (MCMC). Within the MCMC framework, the unobserved locations are removed by Monte Carlo integration thus avoiding the necessity of explicit integration. We adopt a general strategy here based on a method of "data augmentation" (Tanner and Wong 1987).

Data augmentation can be formally motivated by the assumption of a discrete uniform prior on N having support on the integers N = 0, 1, . . . , M for some large M. Under a reparameterization, the model is equivalent (Royle et al. 2007) to physically augmenting the observed data set with a large number, M - n, of ''all zero'' encounter histories. Thus, the size of the data set (M) becomes a fixed quantity, and the model is reparameterized to be technically equivalent to what are sometimes referred to as ''site occupancy'' models (e.g., MacKenzie et al. 2006). While the technical derivation is precise, the augmented zeros are something of an abstraction, corresponding to what one might call ''pseudo-individuals,'' only a subset of which are members of the population of size N that was exposed to sampling. We assert that M is sufficiently large so that the posterior of N is not truncated (this can be achieved by trial and error with no philosophical or practical consequence). Given the augmented data set, we now introduce a latent indicator variable, say z_i; i = 1, 2, ... M, such that $z_i = 1$ if the ith element of the augmented list is a member of the population of size N, and $z_i = 0$ otherwise. We impose the model $z_i \sim$ Bernoulli(ψ), where ψ will be referred to as the inclusion probability. This is the probability that an individual on the list of pseudo-individuals is a member of the sampled population of size N. Under this formulation, the resulting model is a zero-inflated version of the "known-N" model, which provided some of the motivation underlying the formulation put forth by Royle et al. (2007). Specifically, $1 - \psi$ is the zero-inflation parameter, and ψ is related to N in the sense that $N \sim$ Binomial(M, ψ) under the model for the augmented data. This relationship between N and ψ has been noted elsewhere in the context of site occupancy models and closed population size estimation (Karanth and Nichols 1998, Royle et al. 2007).

MCMC methods obtain a sample of the model parameters from the posterior distribution by Monte Carlo simulation. Typically, a large sample of dependent draws from the posterior is obtained after an initial sample (referred to as the ''burn-in'') is discarded to ensure that subsequent draws are being generated from the target distribution…. Within the MCMC framework, the individual activity centers are regarded as missing observations, and they are estimated by Monte Carlo sampling from the posterior distribution (Royle & Young 2008, Royle et al. 2009a).

APPENDIX 3

Guide to enter data for the program Density (Efford, 2007)

Leonardo Maffei, Andrew Noss and Mathias Tobler

NOTE: This guide is not intended to replace the original publication:

Efford, M. G., Dawson, D. K. & Robbins, C. S., 2004. DENSITY: software for analysing capture–recapture data from passive detector arrays. ***Animal Biodiversity and Conservation*****, 27(1)*****:*** **217–228.**
Readers are also direct to the web site: http://www.otago.ac.nz/density/

This guide is intended as support to users on entering the data into the program for analysis. This is not the original Density guide, and is not approved nor reviewed by the program's authors. This guide is based on the program's details that appear in the ***Help*** **button, and any errors belong to Maffei, Noss, and Tobler.**

This guide is divided in two parts: Part 1 explains how to organize the data and how to run the program, and Part 2 explains the details of each window. Be aware that some points are not explained thoroughly.

PART 1. Running the program

The DENSITY program applies methods for density estimation of animal populations from capture and recapture data using a series of 'detectors'. These detectors can be traps for live animal capture and marking specimens, hair traps to obtain DNA samples, or camera traps that take photos allowing individual identification by their natural marks.

The Spatially Explicit Capture Recapture (SECR) methods use the locations where the animal was registered to construct a spatial model of the detection process and then to obtain estimates of the population density. Density calculations are determined estimating the centers of home range of observed animals in the sampling area. The Inverse Prediction (IP SECR) and the maximum likelihood (ML SECR) are alternative methods that help run the spatial detection model.

To run the program, first we need two data matrices:

1. TRAP LAYOUT. This matrix can be constructed easily in an Excel file: in the first column goes the correlative number of the trap, in the second the X coordinate, and in the third the Y coordinate, these last two in UTM. Then the file is saved as Text either in the program Notepad under the format .txt or straight from Excel, saving it as Text delimited by tabs. The file will look like this:

1	576324	7837101
2	575525	7837721
3	574790	7838373
4	573928	7838943
5	573146	7839539

2. CAPTURE DATA. This matrix is also constructed in a Excel file. In the first column goes the session number; that means that for a survey we will put “1”, for a second survey “2”, and so on. To make the analysis simpler and facilitate data management we suggest making a single matrix for each survey, so the first column will be only “1”.
In the second column goes the individual identification, including as many lines as necessary, with one line for each capture of each individual animal (this will depend on the next column). In the third column goes the respective day (consecutively numbered) when the animal was captured. If our study begun on April 1st and the animal was captured on the 20th, we insert a “20” here; but if it was captured on May 10th, we will insert a “40” given that from April 1st, May 10th is day 40 of the survey.

In the last column appears the number of the trap where the animal was captured. This column is the one that relates both matrices, given that is the only one shared by both. It is very important that the trap numbers match with the numbers from the first matrix, which means that all the trap numbers in the second matrix must appear in the first one.

The file will look like this:

1	1	26	40
1	1	26	42
1	1	33	13
1	1	55	12
1	2	38	15
1	2	38	15
1	3	38	2
1	4	10	41
1	4	10	42
1	5	30	10
1	6	55	45
1	7	16	44

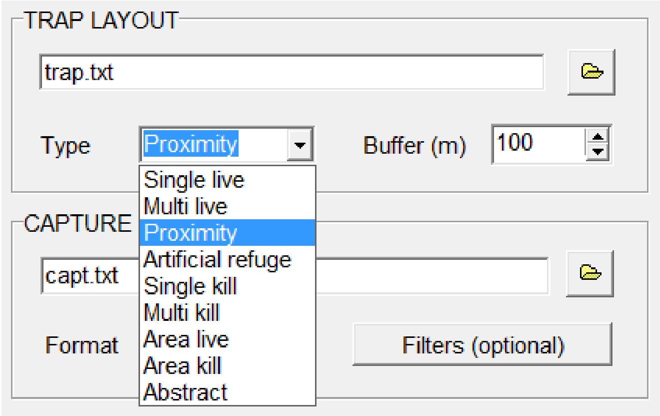
Once the matrices are elaborated, we can run the program.

If you do not have the program, you can download the last version available from:
http://www.mbr-pwrc.usgs.gov/software.html
and save it in a folder labeled for the program.

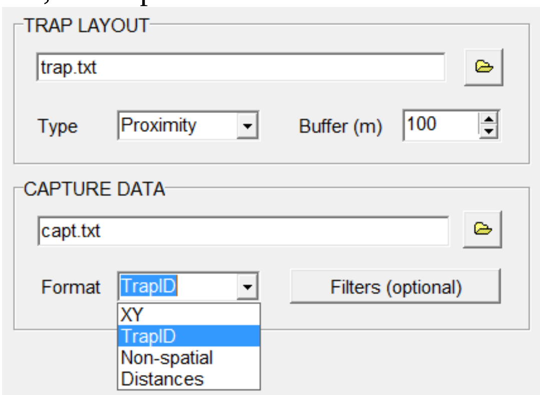
Then open the file and click on the icon density and accept the welcome window.

A window were data are entered will appear. In the TRAP LAYOUT text box area the file .txt with the distribution of traps is inserted and in the CAPTURE DATA text box area the file with capture data is inserted.

In this Windows, there are other capture details to be defined: **Type** is the way animals have been captured. The most common options are: *Single Live*, when the animal is captured, marked and released; *Multi live* where the animal can be captured several times in the same trap; *Single kill* when the animal dies in the capture, as with rat traps; and *Proximity* when the animal is registered but not captured, as is the case with camera traps.



Format: this is how we describe the trap spatial distribution in our files. There are four options. *Trap ID*: where captures are linked with trap locations through the file TRAP LAYOUT, where each station has a number (trap id) and the coordinates. *XY*: an alternative to the former, but in this case each capture is directly related to geographic coordinates. *Non-spatial*: when there are no coordinates for capture sites, but in this case density cannot be calculated, only abundance. *Distances*: this format works with the distances between captures. We recommend working with the two matrices described mentioned above, so Trap ID must be selected.

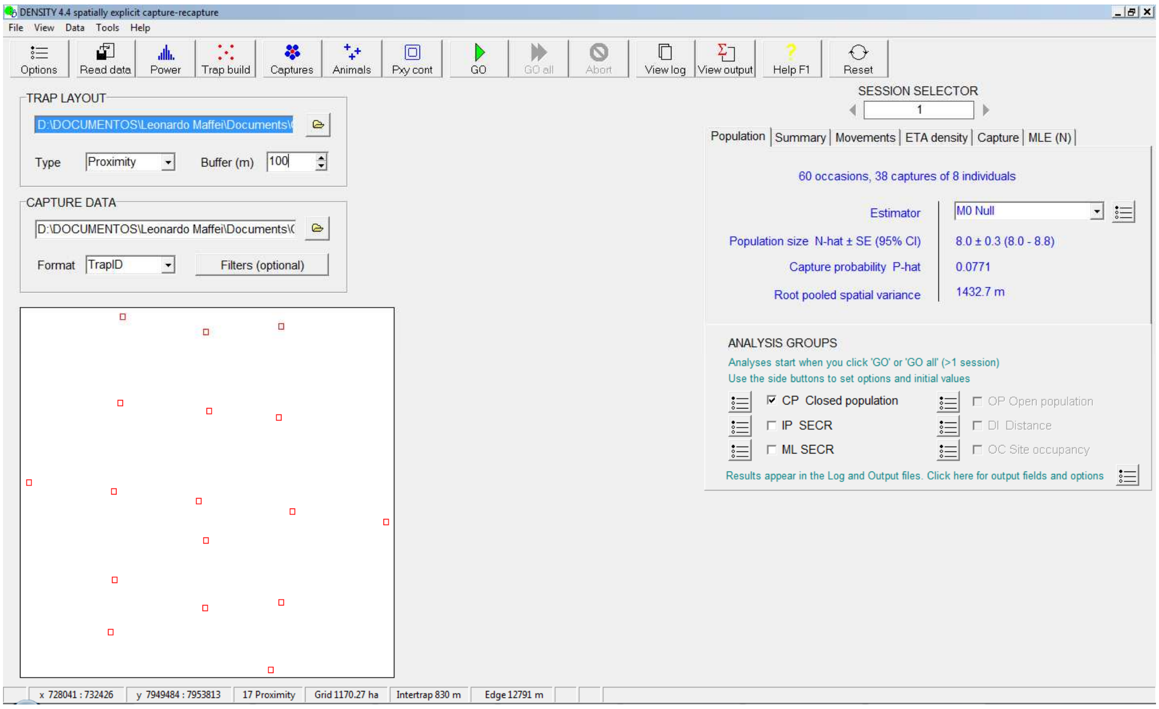


The text box area *Buffer (m)* refers to the buffer that will be added to the traps to create the “state space”, and the default is 100 (because the program was originally developed for small mammals). In the case of large mammal surveys with camera traps, a large value must be inserted; the author (Efford, *pers*. *Com.*) indicates that with this value an analysis area is created in which estimations are run, and it must be larger than the area covered by the traps because the home range centers of the animals registered can fall outside the survey polygon. We suggest multiplying the MMDM by 5 and use this value as the Buffer to run the program (the value MMDM is found in the *Movements* tab after clicking on Read Data).

You can also use an MMDM distance from a similar study or an average home range diameter from radio-tracking (e.g. Approximate radii: hr 10km², radius 1,783m, diameter 3,567m, hr 20km², radius 2,523m diameter 5,046m, 25km² radius 2,820m, diameter 5,640m, 30 sq km radius 3,090m diameter 6,160m, 50km² radius 3.989m, diameter 7,978m, 80km² radius 5,046m diameter 10,092m, 100km² radius 5,642m, diameter 11,284m, 140km² radius 6,676m, diameter 13,351m, 200km² radius 7,979m diameter 15,958m).

Finally we have the *Filters (optional)* tab that allows us to analyze several sessions or captures. As our matrix is from one survey only, we do not change anything.

To see the results in ind/km² enter Options→ Output → Units of Area and select *sq km*. After you have inserted in this window the Trap Layout and Capture Data file names and you have defined *Type*, *Format* and *Buffer*, press Read data to load the data. First it is possible that several windows will appear saying "Duplicates will be ignored"; if so, press accept until they are gone. These messages indicate that some captures will be ignored in the capture-recapture analysis because they were made on the same day.
Then this screen will appear:



In Estimator appears by default M0 Null; change it to Mh Jacknife, because this estimator is more robust. If, however, the latter cannot estimate the density (you will know because in *Population size* and *Capture probability* NA will appear), then return to M0 Null.

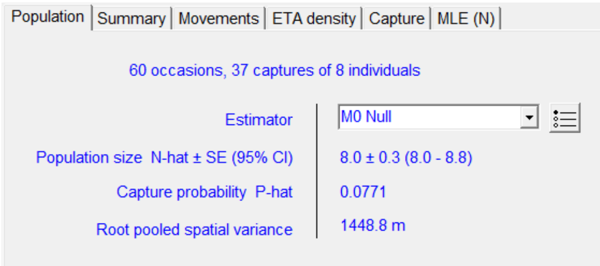
Then, in **ANALYSIS GROUPS** select **ML Secr** only, given that **CP Closed Population** comes by default.

Then run the program by pressing GO. The program will take some minutes to complete the analysis. When in the lower right part of the screen appears DONE and a green circle, the results are ready. The final density calculated through the ML SECR method appears in ind/km² in the lower right of the screen (*Density*).
To know the standard error and the confidence limits, once the data are run, press the View Output tab. A text window will open where all the results of the analysis are detailed. In the last line, titled Output, search for SE.MLDens, LC.MLDens and UC.MLDens. They are together, and these values are the standard error, the lower confidence limit and the upper confidence limit.

Part 2. Details about the components of Density

In the lower left part of the main screen of Density appears a map of the traps, which serves to confirm that we did not make any mistakes entering the coordinates.
On the right side of the main screen appears the results window, with a top menu including six tabs.

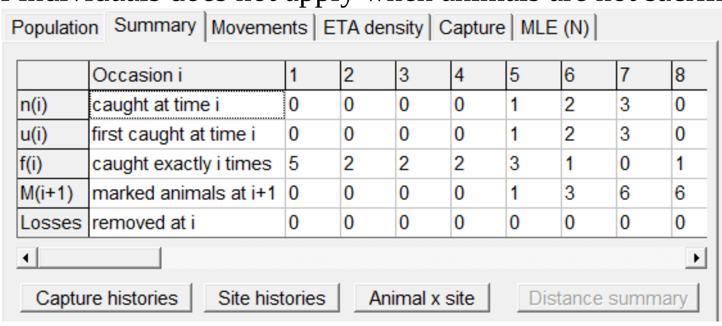
Population: The first tab, that appears when the program is run, shows the general population data:



First you can see the number of trap days, captures and individuals.
Then you have:
Estimator is the statistical model used in abundance estimation through capture-recapture. By default appears the basic estimator M(o).
Population size shows the abundance calculated by the CAPTURE program according to the model (*Estimator*) selected in the previous point, the standard error and the confidence interval.
Capture probability is estimated according to the model selected in *Estimator*.
Root pooled spatial variance: is the average of the variation of localizations around the hypothetical home range centers for every individual.

Summary: The next tab summarizes the captures per day, where:

- *n(i)* is the number of animals captured on that occasion (or on that day for our camera trap study)
- *u(i)* indicates how many animals have been captured for the first time that day
- *f(i)* is the number of captures for each individual, that is, how many individuals have been captured one time, how many two times, etc.
- *M(i+1)* is the cumulative number of captures (in individuals, not records)
- *Losses* of individuals does not apply when animals are not sacrificed



	Occasion i	1	2	3	4	5	6	7	8
n(i)	caught at time i	0	0	0	0	1	2	3	0
u(i)	first caught at time i	0	0	0	0	1	2	3	0
f(i)	caught exactly i times	5	2	2	2	3	1	0	1
M(i+1)	marked animals at i+1	0	0	0	0	1	3	6	6
Losses	removed at i	0	0	0	0	0	0	0	0

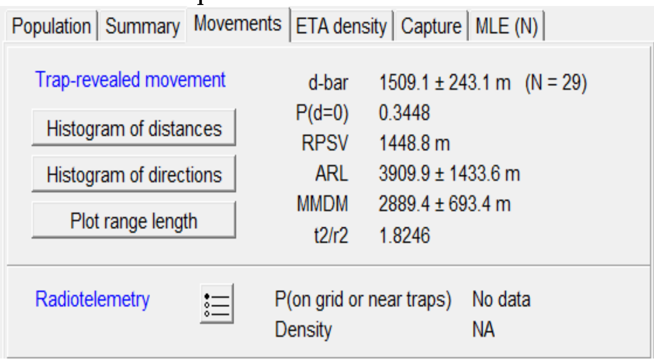
The lower tabs indicate:

- **Capture histories**: the day when each animal was captured (Individual by Occasion)

- **Site histories**: which individuals and on what days were they captured at each trap (Trap by Occasion)
- **Animal x site**: the number of times that every individual was captured in each trap.

Note: to interpret these last data you must have in hand the matrices with the camera trap locations.

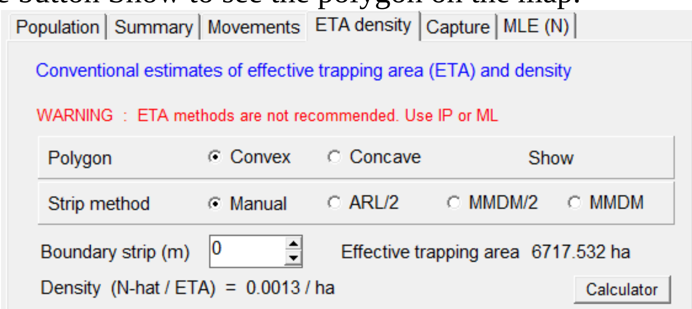
Movements:
d-bar = Mean distance between recaptures
P(d=0) = Proportion of traps with captures
RPSV = Square root of the spatial variance
ARL = Asymptote Range Length in meters (this is another estimation of the MMDM and the diameter of home range with asymptotes)
MMDM = Mean Maximum Distance Moved by every individual recorded at least in two different traps
t2r2 = the *Schoener Relation* is the relation of the squared mean distance between successive observations and the squared mean distance of the "center of activity"



ETA density: In this tab appears the recommendation to not use the Effective Trapping Area methods (do not use the sampling area estimated from MMDM, see the figure below).
- *Polygon*: First you have to set the edges of the polygon: convex or concave. We suggest using Concave.
- *Strip Method*: Then you must set how the buffer will be added to the sampling area. It can be manual, ARL/2 (this is other way to calculate the sampling area with asymptotes), MMDM/2 and MMDM. If selecting *MMDM/2* does not work, *Manual* must be chosen, which is the default, and in the window *Boundary Strip* write the MMDM/2, or better an MMDM value derived from the data, or other locally relevant data on home range diameter. Press the button Show to see the polygon on the map.

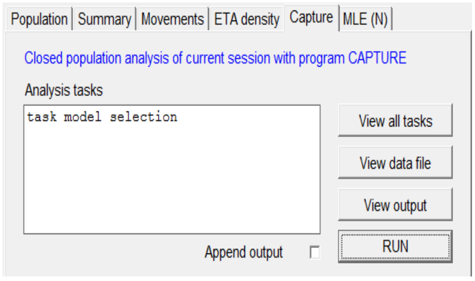
This window shows two main elements of the analysis:

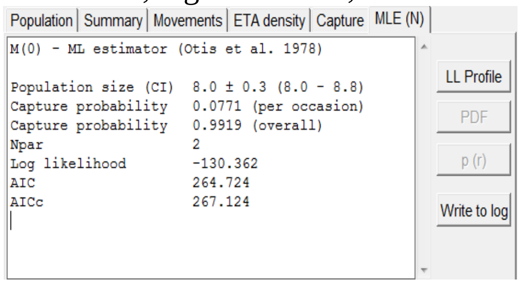
1. *Effective trapping area*
2. *Density* (in individuals per hectare)



One of the greatest advantages of DENSITY is that here the survey area and density are calculated very quickly, applying all the models that CAPTURE uses, and with all the possible buffer values (1/2 MMDM, MMDM, radiotracking, etc.)

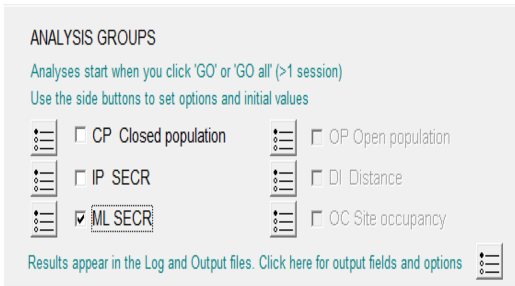
Capture and **MLE (N)** – the last one in some versions only:
Capture is to run data with the Capture program and *MLE(N)* gives more details about the results of classic models in DENSITY like AIC, log Likelihood, etc.



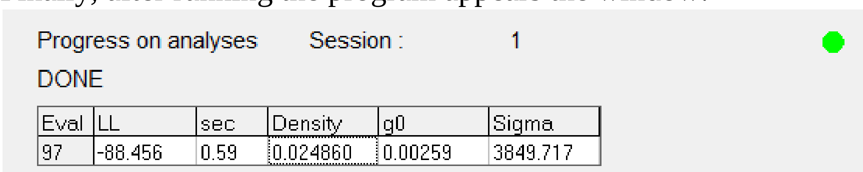


ANALYSIS GROUPS:
In the lower part of these Windows we just reviewed, a window with three commands to run the Density program is found:

CP Closed population
IP SECR: Density estimated from Inverse Prediction
ML SECR: Density calculated from Maximum Likelihood.
You will find here also an option to analyze open populations.



Finally, after running the program appears the window:



Where:
Eval: Number of iterations made to estimate density (many iterations are run because density is estimated with different values of analysis parameters [such as different sets of possible home range centers for individuals recorded in the sampling area], every time narrowing in on the final result. When variation is minimal between iterations, the program is done).
LL: Maximized log likelihood.
sec: Seconds the program took to produce the results.
Density: of the species in ind/km².
g0: capture probability when the trap and the activity center coincide.
Sigma: a range parameter that approximates home range diameter

APPENDIX 4

Guide to enter data for the program Secr (Efford, 2011)

NOTE: This is a simple guide only for entering the data into the program. It does not contain any information on its scientific foundations; for this the reader should refer to the original author: **Efford, M. 2011. Secr – spatially explicit capture-recapture in R. Manuscript.** Readers are also directed to the web site: http://www.otago.ac.nz/density/SECRinR.html

Step 1.
Construct two data matrices:

1. Traps distribution. This can be made easily in an Excel file: the first column is for the correlative trap number, the second for the X coordinate, and the third for the Y coordinate, these last two in UTM. Then the data are saved as a .txt file. This can be done in Notepad or directly in Excel saving in the Comma Separated Value format. The file will look like this:

1	576324	7837101
2	575525	7837721
3	574790	7838373
4	573928	7838943
5	573146	7839539
6	572659	7837449
.	…..	…..

2. Capture data. This matrix is also constructed in an Excel file. In the first column goes the session number; that means that for the first survey we will put “1”, for a second survey “2”, and so on. To simplify the analysis and facilitate data management we suggest making a single matrix for each survey, so the first column will be only “1” values.

In the second column goes the individual identification, including as many lines as necessary, with one line for each capture of each individual animal (this will depend on the next column). In the third column goes the respective day (consecutively numbered) when the animal was captured. If our study begun on April 1st and the animal was captured on the 20th, we insert a “20” here; but if it was captured on May 10th, we will insert a “40” given that from April 1st, May 10th is day 40 of the survey.

In the last column appears the number of the trap where the animal was captured. This column is the one that links both matrices, given that is the only one shared by both. It is very important that the trap numbers match the numbers from the first matrix, meaning that all the trap numbers in the second matrix must appear in the first one.

The file will look like this:

1	1	26	40
1	1	33	1
1	1	55	12
1	2	38	15
1	3	38	2
1	4	10	41
1	4	10	42
1	5	30	10
1	6	55	45

Once constructed, the matrices are saved in an easily accessible file, like the computer's C or D drive.

Step 2.
Run the program:

1. Download R and secr from http://www.r-project.org
2. If you have R as a direct access on your computer, open it. If not, open the file R, enter *bin* and then in *i386* click on *Rgui*.
3. A new window will appear. In the upper menu go to Packages → Install Packages.
4. A new window will appear (if CRAN mirror appears, select a country to connect to). Then select secr and click on OK.
5. This text appears:

Loading required package: abind
This is secr 2.3.0. For overview type ?secr

6. In the remaining window, after the sign > (which is in red), write:
   library(secr)
   →Enter.
7. After the sign > write:
   capthist<-read.capthist('XXX', 'YYY', detector='proximity',fmt='trapID', noccasions=ZZ, skip=1)

Where XXX is the path to the captures matrix and YYY is the path to the trap distribution file. The path of the matrixes will look like this:
'C:\\Documents\\Density\\TrapLocation.txt'
Do not forget to put the simple quotation marks (') at the beginning and end of each route. ZZ is the survey length in days.
→Enter

This line should appear:
No errors found :-)
In this first stage is where most errors are made and the program does not run. The most common errors are assigning the wrong number of days to the survey, a non-valid file path or an incorrect file name.

8. If you wish to see a graphic of your survey, after the sign > write:
plot(capthist,border=3000,tracks=TRUE,varycol=TRUE)
→Enter
A graphic of your survey will appear in an area extending 3000 m around the traps.

9. If you wish to confirm the data entered, after the > write:
summary(capthist)
→Enter
A capture matrix with the summary of the data per sampling day will appear.

10. After the sign > write:
buffer=15000
→Enter

Another sign > will appear, where you have to write:
secr.0 <- secr.fit (capthist , model = g0 ~ 1, trace = FALSE, buffer=buffer) →Enter
The program will spend several minutes processing data.

NOTE: The value of *buffer* here is important, because it will define the area *S* in which the analysis will be run. The user must define this, and it must be large enough for the species studied a minimum of four times *sigma* (see below). Based on data from Kaa Iya National Park in Bolivia, we suggest running a *buffer* of 15000 for species with large home ranges like jaguars or pumas and 6000 for animals with smaller home range like ocelots and tapirs. Then this buffer value can be compared with *sigma* in the results (verifying the buffer is at least four times sigma). If so, the results can be considered as final, if not, the program is run again multiplying the value of *sigma* by four and using this *buffer* in this step. In the case of data from Kaa Iya, initial analyses started with smaller buffers, which were then increased, with density estimates stabilizing at the buffer levels recommended above. Larger buffers offered no improvements. While buffers cannot be too large, the danger would be setting them too small. We have yet to explore separate analyses for males and females using different buffers, primarily due to small sample sizes.

11. After the program stops running, the sign > appears again, after which you have to write:
secr.0 →Enter
A window with the results will appear, and the most important are:

```
Detector type      proximity
Detector number    31
Average spacing    1759.208 m
x-range            724035 738941 m
y-range            7944153 7956164 m
N animals       :  7
N detections    :  22
N occasions     :  65
Mask area       :  112323.9 ha
```

Where:
Detector type was defined when you entered the data and defines the camera traps as proximity detectors, given they do not capture physically the animal nor kill it. They either affect the possibility of capturing the same animal in other traps on the same day or other animals in the same trap on the same day.
Detector number is the number of traps or stations.
Average spacing is the average distance among cameras.
X and Y Range are the coordinate ranges in UTM of the camera polygon.
N animals is the number of individuals photographed.
N detections is the number of observations of these individuals.
N occasions is the survey length, in days for this example.
Mask area is the analysis area, including the *buffer*.

At the end of results, you see:

```
Fitted (real) parameters evaluated at base levels of covariates
       link     estimate  SE.estimate          lcl          ucl
D       log 1.192138e-04 5.667549e-05 4.921381e-05 2.887791e-04
g0    logit 1.142273e-02 4.319588e-03 5.429843e-03 2.387117e-02
sigma   log 4.094811e+03 8.330980e+02 2.759358e+03 6.076586e+03
```

Where:
D is the density.

g0 is the detection probability.
sigma is a range parameter approximating the registered species' home range diameter, in this example, 4,049 meters (data that are used to corroborate the *buffer* explained above).
In the density data (*D*), the first column (*estimate*) is the density itself, the second column (*SE.estimate*) is the standard error, the third column (*lcl*) is the 95% lower confidence limit and the fourth column (*ucl*) is the 95% upper confidence limit. Be aware that all these data are in hectares, and you must multiply them by 10,000 to convert them into individuals per 100 km^2. In our example the density 1,19…e-04 is 0.000119 inds/ha, multiplied by 10,000 becomes 1.19 inds/100 km^2.

APPENDIX 5

Guide to enter data for the Spacecap (Gopalaswamy, 2012)

NOTE: This is a guide only for entering the data into the program.
It does not contain any information on its scientific foundations; for this the reader should refer to the original authors:

Arjun M. Gopalaswamy, Andrew J. Royle, James E. Hines, Pallavi Singh, Devcharan Jathanna, N. Samba Kumar and K. Ullas Karanth (2012). Program SPACECAP: software for estimating animal density using spatially explicit capture-recapture models. Methods in Ecology and Evolution. doi: 10.1111/j.2041-210X.2012.00241.x

Preparing the data:

First you must construct three data matrices:

1. Details on species' capture. This matrix can be produced in an Excel file with three columns: LOC_ID is the number of the trap where the animal was captured or photographed, ANIMAL_ID is the individual identification and SO is the day when the animal was captured.

In this matrix from a camera trapping survey, for example, individual 1 was photographed at trap 24 the seventh day of sampling. Then it was photographed at trap 4 the eighth day of sampling

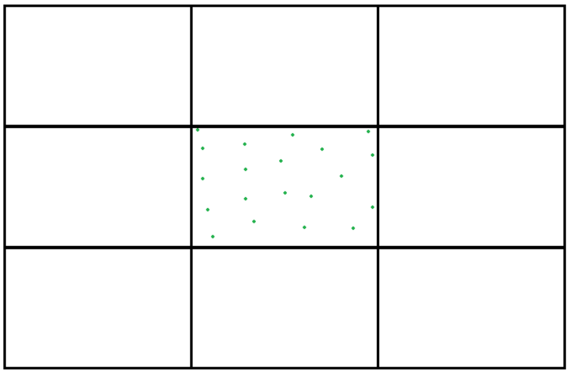
	A	B	C
1	LOC_ID	ANIMAL_ID	SO
2	24	1	7
3	4	1	8
4	3	1	8
5	2	1	8
6	.	.	.
7	.	.	.
8	.	.	.

2. The details of trap distribution and the days they were functioning. LOC_ID is the number assigned to each camera trap and is related to the previous matrix, and X_Coord and Y_Coord are the coordinates of the traps in UTM. Then insert one column for each day of the survey (or one column for each capture occasion) and in the matrix insert a 1 for the days when the trap was on and a 0 when the trap was off.

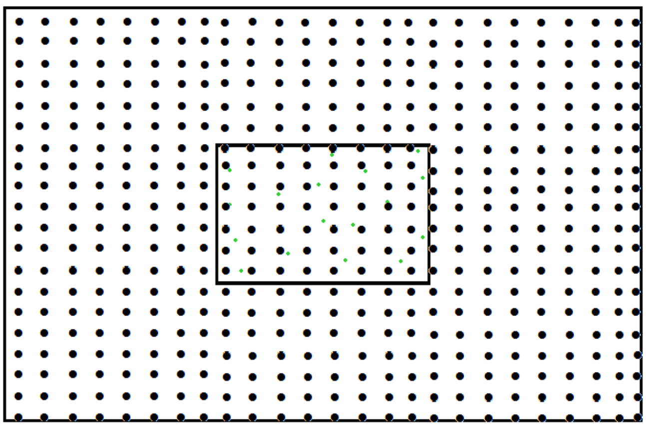
	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	R	S	T
1	**LOC_ID**	**X_Coord**	**Y_Coord**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**.**	**.**	**.**	**55**	**56**	**57**	**58**	**59**	**60**
2	1	628767	7963185	1	1	1	1	1	1	1	1	.	.	.	1	1	1	1	1	1
3	2	627087	7963366	1	1	1	1	1	1	1	1	.	.	.	1	1	1	1	1	1
4	3	625986	7963462	1	1	1	1	1	1	1	1	.	.	.	1	1	1	1	1	1
5	4	624602	7963600	1	1	1	1	1	1	1	1	.	.	.	1	1	1	1	1	1
6	5	622801	7963770	1	1	1	1	1	1	1	1	.	.	.	1	1	1	1	1	1
7	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
8	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
9	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
10	24	627778	7964854	1	1	1	1	1	1	1	1	.	.	.	1	1	1	1	1	1
11	25	623991	7967396	1	1	1	1	1	1	1	1	.	.	.	1	1	1	1	1	1
12	26	634800	7964846	1	1	1	1	1	1	1	1	.	.	.	1	1	1	1	1	1

In the matrix above, for example, we have 26 traps and the survey lasted for 60 days. As all the days are identified by a 1, that means that all the traps were functioning throughout the entire survey.

3. Potential home range centers. This is a matrix with equidistant points that simulate the hypothetical home range centers of the individuals of the species we are studying in the sampling area. The area (S) covered by these points has to be very large to avoid any possible limiting effect of the area covered by the traps in relation to the real home range of the species. The program will run thousands of iterations, selecting sets of hypothetical home range centers and comparing them with the actual observations during the survey to estimate the number of home range centers associated with the area S, and at the same time, the density. We can, for example, make a rectangle covering all the camera traps of a survey (green dots below) and then we add this same area around the camera traps. The boundaries of S would be:



Then add the grid of hypothetical points, all equidistant, something that will look like this:



IMPORTANT: hypothetical points must be spaced apart a distance less than the average distance between the traps. For example, 1 or 2 km among points vs. 4 km among camera traps in a jaguar survey.

GIS programs generate automatically this kind of matrix from the rectangle's four corners and the distance among points set by the user. The final matrix in Excel will look like this:

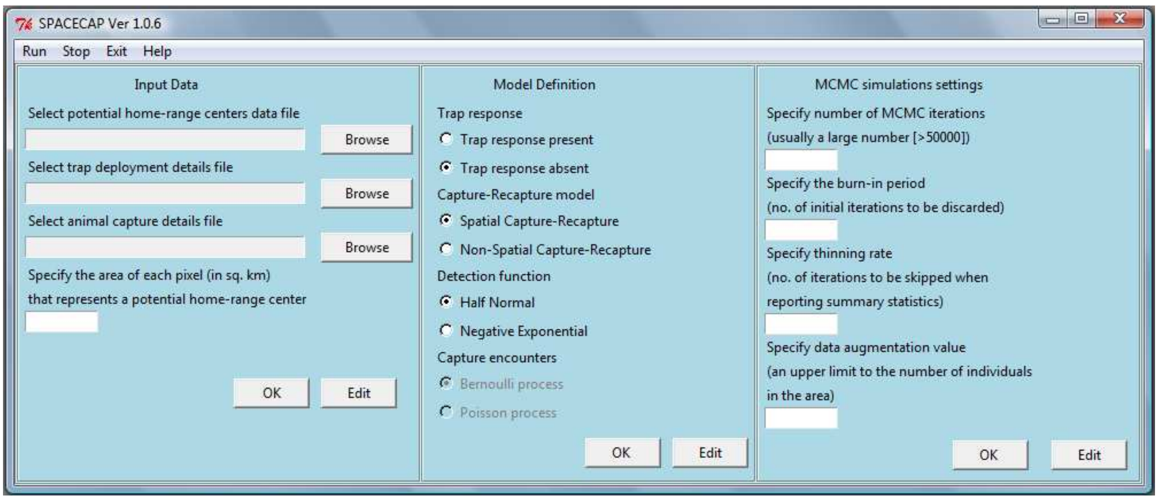
	A	B	C
1	X_COORD	Y_COORD	HABITAT
2	604000	7983000	1
3	606000	7983000	1
4	608000	7983000	1
5	610000	7983000	1
6	.	.	.
7	.	.	.
8	.	.	.
128	616000	7973000	1
129	618000	7973000	1
130	620000	7973000	1

Here, columns A and B are the coordinates and C the habitat type. As these data come from a homogeneous area, only 1 appears in the habitat column; if we had several kinds of habitat, we would put 2, 3, 4… depending on the habitat where each hypothetical point falls.
For animals with small home ranges, like ocelots or tapirs, we suggest a separation of 0.5 km between points; and for animals with larger ranges, like jaguars or pumas, a separation of 1 km. Depending on the area covered by the traps, this matrix can include 1000 points or even more.

IMPORTANT: After these three matrices are constructed in Excel, they should be saved as .CSV (Comma Separated Value) files.

To run the program:

12. Download R and Spacecap from http://www.r-project.org.
13. If you have R as a direct access on your PC, open it. If not, open the file R, enter to *bin* and then in *i386* click in *Rgui*.
14. A new window will appear. In the upper menu go to Packages → Install Packages.
15. A new window will appear (CRAN mirror), select a country to connect to, yours or a neighbor. Another window will appear, select SPACECAP and then click on OK.
16. In the top menu go to Packages → Load Packages and open Spacecap.
17. In the remaining window, after the sign > (which is in red), write: SPACECAP() →Enter.
18. A new screen appears:



This screen has three parts:

Input Data
In the first text box (*Select potential home-range centers data file*) the file with the potential home range centers is entered, pressing Browse to locate it on your computer.
In the second text box (*Select trap deployment details file*) the file with the camera trap locations is entered.
In the third text box (*Select animal capture details file*) goes the capture data file name.
In the fourth text box insert the mesh size for the grid of the potential home range centers. If the points for jaguar/puma are separated by 2 km, here we put 4 (2 km x 2km); if they are separated by 1 km, we put 1 (1 km x 1 km) and if the points are separated by 0'.5 km (0.5 km x 0.5 km) we put 0.25.
Select →OK

Model Definition
That initially is left with the default selections.
"Trap response absent" means that traps do not provoke a negative reaction by the animal to the method of capture where it will avoid being captured in the future. "Spatial capture recapture" is the spatial analysis we want to run. Currently SPACECAP only runs the "Half-normal" detection function and the Bernoulli encounter process .
Select →OK

MCM simulations settings
Specify number of MCMC iterations: it is recommended to put 50,000 iterations, which will take 6 hours or more. To ensure the program is working well, you can make a practice run with 1,000 iterations.
Specify the burn-in period: when you make a test with 1,000 iterations, you can insert 100; for real density estimations with 50,000 iterations, you can insert 1,000. This value is the number of initial iterations that will be deleted as possible outliers while the program establishes reasonable parameter ranges.
Specify thinning rate: here you can insert 1, and all iterations will be considered.
Specify data augmentation value: the authors suggest a value 5 – 10 times the number of animals observed in the survey. If we are analyzing repeated surveys, we can standardize this value. For example we can always use 50 when 5 – 10 individuals have been observed.
But you can confirm that the data augmentation value is sufficiently large by comparing with "Nsuper 95% upper HPD level" (see below in results): this number should not be larger than *data augmentation value*. If it is larger, then the data augmentation value is artificially limiting the upper bound of the iterations, and density will likely be over-estimated.
Select → OK

Finally go to the tab on the upper left of the screen and click Run

After the program has processed the data (which can take hours, and you can monitor progress as the results of each iteration are listed in turn on the Spacecap screen, while a separate window opens to show a progress bar), it produces a folder of results that includes graphs of the parameter values, a complete list of the results by iteration, and the summary results as follows:

_	Posterior_Mean	Posterior_SD	95%_Lower_HPD_Level	95%_Upper_HPD_Level
sigma	2.4206	0.4544	1.7206	3.3227
lam0	0.0148	0.0025	0.011	0.0194
psi	0.7531	0.1708	0.4411	0.9986
Nsuper	22.26	4.9168	13	29
Density	1.1042	0.2439	0.6448	1.4385

Sigma represents a "movement parameter" for our study species, and must be converted to meters using this formula: √(sigma/2) * 5000. In our example, we have √(2.4206/2) * 5000= 5500 m.
This distance in meters is an estimation of the average home range diameter for our study species in the sampling area.
lam0 = 0.0097 is the encounter rate in trap "j" on day "k" of an individual "i" whose home range center is exactly at that trap location.
psi is the relation of the number of animals present in the analysis area S (the area covered by the hypothetical home range centers) to the maximum possible augmentation value set by the user.
Nsuper is the population size – the number of activity centers in the area S.
Density is equal to Nsuper / S, where S is the analysis area. In this example, it is reported directly as 1.1 individuals / 100 km^2.

IMPORTANT:

- The value of *95%_upper_HPD_Level* of Nsuper must **NOT** exceed the *Data augmentation value* (the last number set in ***MCMC simulations settings,*** which was 25). In our example is 29, so the analysis is OK, given that when we ran the program we set 50 in *Data augmentation value.* If we had set 25, we should run the program again with a *Data augmentation value* larger than 29.
- The makers of SPACECAP recommend a minimum of 50,000 iterations (*MCMC iterations*) and we have not used larger values because of time required for the analysis (4 hours in a jaguar survey with few captures and more than 50 hours in other cases).
- The value of the *burn-in period* can be altered if the user wants to increase the number of initial iterations that will be eliminated.
- The value *thinning rate* is the number of iterations that will be taken into account. If we put 1 in this box, all iterations will be saved. If we put 2, the second iteration will be saved, discarding the first (that means 50% of the iterations). If we put 3, the third iteration will be saved discarding the first two and so on.

APPENDIX 6

The ability to detect change - statistical power analyses

Statistical power is the probability of detecting a significant effect or trend, despite "noise" such as natural variation. Statistical power increases as sample size increases, and as variance decreases. Power analyses evaluate the probability that monitoring will detect a change in the event of authentic change (1-β), in relation to the probability that monitoring will detect a change when there is no change, or a type 1 error (α), in other words, **Power is the capacity to detect real change when it occurs, THE goal of monitoring.**

Power analysis needs 1) number of sampling occasions/extent of effort, 2) the set rate of increase or decrease to measure, 3) a coefficient of variation of the measurements not attributable to the effect of interest (measure of precision afforded by the natural system), 4) a α significance level (the standard used to reject the null hypothesis), which can result in a calculation of power (1-β) (Hatch 2003). One trade off is that it might be better to detect false change, versus missing change. If decline is of paramount importance, tests should be one-tailed, and α not set too low.

An example follows, using track surveys of endangered Siberian tigers. Hayward et al. (2002) evaluated a track survey program that would provide over 80% power to detect declines of 10% with a 20% chance of type 1 errors (α). Hayward et al. (2002) used the program Monitor, examining the capacity to detect change over 5 years. Standard deviations (natural variation) were calculated on a mean track index from 15 survey areas. Information from data-in-hand went into these decisions. The authors concluded that power was increased by extending route length (which reduced variance), and that power was increased by increasing numbers of routes (e.g. from 3 to 10). Longer routes resulted in decreased variance and less routes with zero counts. Reducing the sample would not permit detections of declines of 10%.

The authors cited Kendall et al. (1992), and Beier and Cunningham (1996) as defending a type one error rate of 20% as a reasonable compromise in endangered species monitoring. These authors were able to use preexisting data to calculate effort needed to provide over 80% power, to detect a 10% annual decline, with a 20% chance of "false alarms". The above example does not translate directly to camera trapping, but illustrates the value of building and layering foundations rich in data, and the demands that documenting trends with confidence can place on researchers.

Trend Analyses

Two programs for analysis of trend data are MONITOR and TRENDS (Hatch 2003). Monitor Version 11. 2010 is available at
http://www.esf.edu/efb/gibbs/monitor/monitor.htm.

TRENDS software is available at
http://swfsc.noaa.gov/textblock.aspx?Division=PRD&ParentMenuId=228&id=4740
(Gerrodette, T. 1987, 1991)

Gerrodette (1987) stated the detection of a trend has five parameters: 1) the number of samples: 2) the rate of change of the quantity being measured: 3) the coefficient of variation, which is a measure of precision, and alpha (α), and beta (β); the probabilities of Type 1 and Type 2 errors.

Power analysis is made with these parameters: duration/extent of sampling, rate of change, precision of estimates, alpha, and power which is 1-beta, where beta is the type 2 error rate, β in which monitoring does not detect change when real change has occurred. The value of any one of these can be estimated if the other 4 are specified.

Power analysis needs input from similar studies, or pilot studies – to generate prescriptions applicable to the study area and species in question. Using simulations based on other sampling efforts might be valid, if sampling practices and natural conditions are identical as for the area for which the power analysis is being conducted.

The U.S. Geological Survey's Patuxent Wildlife Research Center has prepared a Management Monitoring Manual, http://www.pwrc.usgs.gov/monmanual/ a public resource with relevant guidance contained in the section titled Management Monitoring Manual/Setting Sample Size, http://www.pwrc.usgs.gov/monmanual/samplesize.htm.

The USGS site suggests that any calculation of how many samples are needed should be treated as an educated guess. Statistical power and the true optimal number of samples can only be calculated once data has been collected for several years.

The simplest prescription for ascertaining trends is repeated measures in the same locale using methods comparable across the sampling events. This will build the data base, and increase understanding of ecological dynamics, and jaguar status in that area.

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