WildCAM Network Camera Trapping Best Practices Literature Synthesis

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Methodology

A literature review was performed using Google Scholar to look for papers published between 2010 and the present (2019) to obtain what is hoped to be much of the recent literature on camera trap best practices. Previously, a list of themes thought to be integral to a best practices document for camera trapping had been produced, centered around the steps of a camera trapping study: study design/placement, data processing, data analysis, and results reporting. These themes (refer to the list after methodology) were used to focus search results- as such, the Boolean operators and terms (camera trap* OR remote camera*) AND (wildlife OR animal*) were used in conjunction with the following list of terms and operators (always joined to the previous terms with AND)

Order of Search	Terms and Boolean Operators
1	(best practice* OR recommendation* or improve* OR guide*)
2	(problem* OR constraint* or limit*)
3	(lure* OR attractant* or bait*)
4	(metadata OR report* or bait*)
5	(imperfect detection OR detection probability*)
6	power analysis*
7	(sampling unit* OR independence*)
8	(data process* OR metadata standard* OR data manage*)
9	software
10	(richness OR diversity index*)
11	relative abundance*
12	occupancy*
13	(density* OR absolute abundance*)
14	("Random encounter model" OR "REM")
15	("Royle-Nichols")
16	(spatially explicit capture recapture OR SECR)
17	invasive*
18	(placement OR location* OR spacing)

to produce search terms such as (camera trap* OR remote camera*) AND (wildlife OR animal*) AND (best practice* OR recommendation* or improve* OR guide*). The volume of different searches was necessary as with all of the different factors that one should take into account with a camera trapping project, one search would not capture the expected results within a reasonable amount of pages. These often produced thousands of results, so only the first ten pages of each search were used.

All papers that had to do with best practices, case studies used to investigate a specific aspect of methodology, and general reviews (indicated by their titles and/or abstracts) were retained. Studies that didn't contribute anything to the larger field of best practices were discarded (i.e. studies that just used a previously existing method to estimate a population's state variable). The literature search commenced January 9th, 2019 and was finished by March 21st, 2019.

Papers were then classified in an Excel spreadsheet based on what theme or sub-theme of best practices they fell under, and information such as focal species and type of paper (review, case study, etc.) was recorded. Notes on key relevant takeaways were also recorded, and it was this information that forms the backbone of this annotated bibliography.

The 'data analysis methods' and 'reported findings' papers were set aside to be done at a later date. The current literature review only includes 'study design' and 'data processing' papers, in addition to a collection of overview papers.

Camera Trapping Best Practices Themes

1.) Study design
- a. Type of camera/Settings
- b. Power/sensitivity analysis
- c. How many cameras/how many camera days/ rotation of cameras to new sites
- d. Placement (random vs. non-random at the site level as well as within a site)
- e. Sampling units
- f. Attractants vs. no attractants
- g. Effects of invasivity of camera traps on study objectives (CTs aren't truly non-invasive)
- h. Spacing between cameras- independence or dependence
- i. Setting traps for one sampling objective vs. multiple
- j. Time of year/closure

2.) Data processing
- a. Principles and metadata standards
- b. Software
- c. Defining event independence

3.) Data Analysis Methods
- a. Population density/absolute abundance
  - i. Capture-recapture with ad-hoc calculation of effective sampling area
  - ii. SECR and related models (for partially- and un-marked populations)
  - iii. REM
  - iv. Royle-Nichols models
- b. Occupancy
- c. Species richness and diversity
  - i. Observed species richness
  - ii. Estimated species richness
  - iii. Species diversity indices
  - iv. Beta diversity
- d. Population indices
  - i. Relative abundance indices
- e. Others less commonly studied (behaviour, disease, demographics)

4.) Reporting findings (what values, statistics, and information on sites and methodology should be reported)

Annotated Bibliography

1. Overview Papers

Apps, P. J., & McNutt, J. W. (2018). How camera traps work and how to work them. *African Journal of Ecology*, *56*(4), 702-709.

- An overview of the use of camera traps for those who have never used them before. Starting with the very basics, topics such as what media can be produced by cameras, setting them up, and how they work are covered. This paper can be used as a quick crash-course on the very basics of camera trapping.

Caravaggi, A., Banks, P. B., Burton, A. C., Finlay, C. M., Haswell, P. M., Hayward, M. W., Wood, M. D. (2017). A review of camera trapping for conservation behaviour research. *Remote Sensing in Ecology and Conservation*, *3*(3), 109-122.

- Reviews the use of camera traps for ethological studies. The review is focused on three main areas: studying anthropogenic impacts on behaviour, incorporating behavioural responses into management, and studying indicators such as daily activity patterns.

Glover-Kapfer, P., Soto-Navarro, C. A., & Wearn, O. R. (2019). Camera-trapping version 3.0: Current constraints and future priorities for development. *Remote Sensing in Ecology and Conservation.*

- Conducted a survey of the global camera trapping community to identify constraints affecting the technology's use, opinions on the most-wanted technological innovations for camera traps, compare performance of different brands, and gather information to help formulate a vision of the next generation of camera trapping studies and technology (called camera trapping 3.0). Results suggest main current constraints are cost, theft, and performance in terms of trigger speed and sensitivity- refer to paper for comments and suggestions on dealing with those constraints, as well as other identified issues. Most-wanted technological developments were also increased performance (via better trigger speed and sensitivity) as well as increased environmental resistance and automatic filtering out of misfires. Perhaps surprisingly, there were high levels of variance in user-ratings for camera trap manufacturers and there was no trend in ratings over time. An outline of the future of camera trapping then follows, with suggestions being that trigger speed should be greatly increased, sensor sensitivity and function should be improved (especially with the use of on-board detection algorithms to reduce things like misfires), resistance to extreme environments be improved, that transmission of data is wireless, that there is the ability to create networks of connected sensors, that there be increased automation of processes, and better collaborative tools for the management and analysis of data produced. This paper offers insights into current problems that should be taken into consideration for camera trap surveys as well as an understanding of the direction that the field is moving.

Hofmeester, T. R., Cromsigt, J. P., Odden, J., Andrén, H., Kindberg, J., & Linnell, J. D. (2019). Framing pictures: A conceptual framework to identify and correct for biases in detection probability of camera traps enabling multi-species comparison. *Ecology and Evolution.*

- An important paper for dealing with biases in detection probabilities, one of the largest problems in the field. A literature review was performed, in addition to the use of author experience, to compile factors that affect the detection probabilities of vertebrates. The paper presents an overview of those factors, grouping them into categories such as animal characteristics, camera trap model specifications, camera trap set-up protocol, and environmental variables. It also presents them within a framework to define the processes explicitly at different scales to allow for accounting for these biases.

Rovero, F., Zimmermann, F., Berzi, D., & Meek, P. (2013). "Which camera trap type and how many do I need?" A review of camera features and study designs for a range of wildlife research applications. *Hystrix*, *24*(2).

- An important foundational paper that provides an overview of choosing a camera trap model, an outline of sampling design and features necessary for different camera trapping studies, and a review of current models (at the time of publication).

Sollmann, R., Mohamed, A., & Kelly, M. J. (2013). Camera trapping for the study and conservation of tropical carnivores. *Raffles Bulletin of Zoology*, *28*, 21-42.

- An overview paper specifically focused on the use of camera trapping for the study and conservation of tropical carnivores. Regardless of its focus, it still presents a solid walkthrough of camera trapping, from study design and deployment to analysis, and can still be useful for camera trappers in British Columbia.

Trolliet, F., Vermeulen, C., Huynen, M., & Hambuckers, A. (2014). Use of camera traps for wildlife studies: A review. *Biotechnology, Agronomy, Society and Environment*, *18*(3), 446-454.

- Another overview paper that reviews the basics of camera trapping. It includes an overview of the technical aspect of camera traps, the ways in which camera traps can be used, and data analysis.

Wearn, O., & Glover-Kapfer, P. (2017). Camera-trapping for conservation: A guide to best-practices. *WWF-UK: Woking, UK.*

- A roughly 200 page best practices document produced by the United Kingdom branch of the World Wildlife Fund, this is the recommended document for any newcomer to the field to get a solid crash-course in the use of camera traps. Through thirteen chapters, the document reviews every stage of a camera trapping study, from choosing a model through to analysis and reporting of results. It also includes chapters on the history of camera trapping, what they have been used for to date, and miscellaneous tips and tricks in addition to many helpful diagrams and comparison charts.

1. Study Design

1.1 Type of Camera

Summary: Camera model is often the first question to be asked for a potential camera trap study. However, many prominent overview papers and guides suggest that study questions should precede camera trap model choice, as necessary model specifications can vary depending on study type (Rovero et al., 2014; Wearn & Glover-Kapfer, 2017). With study questions and variables decided, in general, the most important features are some combination of trigger speed, flash type, detection zone, number of photos taken/recovery time, sensor sensitivity, flash sensitivity, power sensitivity, image resolution/sharpness/clarity, camera housing, and camera programming depending on the objectives (Rovero et al., 2014; Wearn & Glover-Kapfer, 2017). Trigger speed, detection zone, recovery time, and battery life have been singled out as being most important generally (Trolliet et al., 2014). Review papers such as Rovero et al. (2014) or chapter four of Wearn & Glover-Kapfer (2017) can provide an in-depth look at camera choice. Two papers, Newy et al. and Wellington et al. (2014; 2014), caution against the attractiveness of the less expensive 'recreational' models, at least without first testing them and considering their suitability for the study. Both suggest that the trade-off of quality for lower cost can be quite high, but the papers can help practitioners consider some of the trade-offs and drawbacks of different models and model quality in more detail.

Newey, S., Davidson, P., Nazir, S., Fairhurst, G., Verdicchio, F., Irvine, R. J., & van der Wal, R. (2015). Limitations of recreational camera traps for wildlife management and conservation research: A practitioner's perspective. *Ambio, 44*(4), 624-635.

- In addition to presenting results of a survey which show that many practitioners continue to use more affordable, 'recreational' camera traps rather than more rigorous, expensive

‘professional’ units, two case study experiments were performed to evaluate the differences between them. The main problems were found to include higher rates of false positive accumulation and higher rates of false negative accumulation. The authors argue that to assess the trade-offs of quality vs. cost, it is important to have a good understanding of the drawbacks of different quality cameras. This study can potentially help practitioners consider some of the trade-offs and drawbacks of different models and model quality.

Rovero, F., Zimmermann, F., Berzi, D., & Meek, P. (2013). “Which camera trap type and how many do I need?" A review of camera features and study designs for a range of wildlife research applications. *Hystrix, 24*(2).

- An important foundational paper for choosing cameras, deciding on quantity, and how to use them. The authors underline that a clear research question must precede camera choice. Other factors that will affect choice are outlined as target species, accessibility, climate, target site, habitat, etc. Cameras are evaluated in the paper based on the following features for choice: trigger speed, flash type, detection zone, number of photos taken/recovery time, sensor sensitivity, flash sensitivity, power sensitivity, image resolution/sharpness/clarity, camera housing, and camera programming. The relative importances however are outlined as depending on study design: faunal detections require generally high sensitivity, fast trigger speeds, wide detection zones, and good autonomy; occupancy studies need fast trigger speeds and high sensitivity, although that depends on species to some extent; mark-recapture studies for density or abundance require white flashes, short recovery times, and high trigger speeds; random encounter models for density or abundance estimates require fast trigger times and large detection zones, no-glow flashes, and cameras that can take bursts of photos. Refer to the paper for a more in-depth exploration of what is outlined above.

Trolliet, F., Vermeulen, C., Huynen, M., & Hambuckers, A. (2014). Use of camera traps for wildlife studies: A review. *Biotechnology, Agronomy, Society and Environment, 18*(3), 446-454.

- Another camera trapping review paper. The paper includes a review of cameras' technical aspects. Among the most prominent qualifications, trigger speed is noted as being crucial to consider; when not using bait or when capturing animals that are slow moving, a trigger speed as fast as possible to capture animals as wildlife cameras do not have wide angle lenses. Detection zone area is also noted as being important: it should always be as large as possible to increase the chances of capturing something that moves in front of the camera. Recovery time is also very important depending on the study and is something that varies greatly- for identifying individuals and behaviors, a short recovery time is extra important. Finally, battery life in general should be as long as possible, but if cameras can be checked frequently cheaper prices may outweigh a longer battery life.

Wearn, O., & Glover-Kapfer, P. (2017). Camera-trapping for conservation: A guide to best-practices. *WWF-UK: Woking, UK.*

- Another review paper. Similar recommendations to that of Rovero et al. (2013).

Wellington, K., Bottom, C., Merrill, C., & Litvaitis, J. A. (2014). Identifying performance differences among trail cameras used to monitor forest mammals. *Wildlife Society Bulletin, 38*(3), 634-638.

- Two types of cameras with substantially different features/specifications were compared by placing one of each type facing the other in the field. The Reconyx model, which had a larger detection zone and higher sensitivity sensor, was found to have recorded twice as many independent captures as the other model. Though camera models change rapidly, this study is an empirical example of the importance of camera features. The results also suggest that it may be a good idea to either test the characteristics of cameras before deploying them if using multiple models, or to use a model that incorporates the existence of the different camera models.

1.2 Settings

Summary: Combined with camera model, camera trap settings are what determine what kind of media is produced as well as their quality, which is the foundation of any camera trap survey. However, only two review papers were found to have discussed camera settings at all, and neither in very much detail. Most camera traps have their settings pre-optimized for field placement (Rovero et al., 2013; Wearn & Glover-Kapfer, 2017). However, most models have the ability to manipulate at least some settings to better reflect the needs of a study. Flash intensity and use can be changed to save battery when studying a completely diurnal species, or to save battery if a strong flash isn't needed in closed environments (Rover et al., 2013). Image quality as well as the forced inactive period after a trigger can be reduced or increased, respectively, to preserve memory (Wearn & Glover-Kapfer, 2017). This might be more useful in more productive systems where capture rates can be much, much higher. Whether images or videos are taken depends on the focus of the study as well. Finally, cameras will optimize settings to obtain the best image when triggered, but some manufacturers allow practitioners to weight which of the settings is more important depending on the study (Wearn & Glover-Kapfer, 2017). Prioritizing blur reduction with an increased shutter speed over exposure, for example, might help identify individuals in density estimation studies that require individual identification based on pelage patterns.

Rovero, F., Zimmermann, F., Berzi, D., & Meek, P. (2013). "Which camera trap type and how many do I need?" A review of camera features and study designs for a range of wildlife research applications. *Hystrix*, *24*(2).

- An important foundational paper for choosing cameras, deciding on quantity, and how to use them. Most cameras have their settings optimized for field placement- for example, if cameras have multiple flash strengths they are usually set on the highest setting out of the box- but it may be worthwhile to turn flash off if you are concerned with a completely diurnal species to save battery, or in closed environments flashes might not have to be on their highest settings.

Wearn, O., & Glover-Kapfer, P. (2017). Camera-trapping for conservation: A guide to best-practices. *WWF-UK: Woking, UK.*

- A best practices review document for cameras, settings are only mentioned very briefly. Most camera traps offer the same basic settings that practitioners can alter. Adjusting sensitivity of the sensor may be important when only attempting to study large animals or when sensitivity needs to be high to capture smaller mammals as well. The forced inactive period between successive triggers can be manipulated to avoid filling up memory too fast. Taking images, video, or both can also be chosen depending on the objective of the study, and the quality of whatever is chosen can also be manipulated depending on concerns with memory usage. Cameras will optimize settings to obtain the best image when they are triggered, but some manufacturers allow practitioners to weight which of the settings is more important depending on the study (for example prioritizing a fast shutter speed to reduce blur at the cost of exposure).

1.3 Power/sensitivity analysis

Summary: In the course of this literature review, no papers were found that discussed the use of power or sensitivity analyses to understand study design requirements in order to have the statistical power to answer the study's questions. From discussions with practitioners in the field in designing the literature review, the importance of such preliminary analyses were discussed several times, so it was expected that there would be some publications on the topic. The lack of papers may be because such analyses are sufficiently covered in general statistics textbooks.

1.4 How many cameras?

Summary: Similar to many other aspects of camera trap studies, recommendations for camera quantities vary notably based on study goals as well as focal species as well as individual study designs, etc. Because of that, only one best practices document, Wearn & Glover-Kapfer (2017), give explicit and generalized guidelines for minimum numbers of camera traps necessary depending on study metric. The document suggests less than 20 cameras is unfeasible for species richness surveys, with 50 locations being a better target. It also notes that there are no hard rules for surveys used to produce relative abundance index surveys, though an increase in sampling locations increases precision. Precision is noted to be much improved when sampling at least 20 locations, and it is best to have more than 50 locations. For capture-recapture models, it is suggested to expose at least 5-10 individuals to sampling, for a naïve recommendation of 40-120 cameras when the separate suggestion of placing 4 cameras per home range is taken into account. For random encounter modelling, it is generally recommended to sample at least 20 locations, with ideally more than 50. Recommendation for occupancy depend on detection probability: for species with detection probabilities of at least .8, species can be detected with 30 sites or slightly less, however many species will need 30-60 sites while rare low-density species with detection probabilities less than .1 will need at least 100 sites.

Rovero et al. (2013), is in agreement with Wearn & Glover Kapfer (2017) in its recommendations for random encounter model studies. A much more common way to discuss cameras is to frame it in terms of however many are needed to capture enough animals for the necessary statistical power for one's models; for example, Rovero et al.'s suggestion to capture between ten and thirty individuals for capture-recapture surveys for density estimation. This underlines the importance of understanding focal animal(s)' characteristics that are important for optimizing camera trapping studies: home range size, detectability, etc. In general, what is necessary for camera trap studies to be successful is the product of the quantity of cameras and how long they are out for, producing a metric known as camera days or camera nights. Because it is a product, the amount of cameras can in general be left in the field for longer and vice versa, meaning there is no one number of necessary cameras, even for studies that are all producing the same state variable estimation (O'Connor et al., 2017; Rovero et al., 2013; Wearn & Glover-Kapfer, 2017). Colyn et al.'s (2018) results underline that a combination of camera density, spacing, total survey effort, and spatial coverage that combine to produce acceptable species richness estimates. Combined with a need for closure, this will result in some minimum number of cameras to be placed that will ensure proper density, acceptable levels of survey effort, spatial representation, and maintenance of closure. These needs are encompassed within the guidelines mentioned above in Wearn & Glover-Kapfer's best practices review document, but for a more in-depth review either reviewing that best practices document or reading sections 1.5, How Many Camera Days? And 1.12, Timing/Length of Study will help.

The number of cameras will be restricted by logistical constraints, but more cameras in general will lead to more precise results (O'Connor et al., 2017; Palmer et al., 2018). One meta-analysis did indicate that placing more cameras did negatively influence relative abundance indices, though the authors suggest that was due to researchers increasing density of cameras when they had more of them rather than a direct effect of the number of cameras (Anile & Devillard, 2016). Spatially explicit capture recapture models were the only models shown to be quite robust to small camera quantities, with just spacing cameras farther out being a more efficient way to increase precision (Sollmann et al., 2012). It has also been shown that it is better to utilize more cameras than increase study length (O'Connor et al., 2017).

Anile, S., & Devillard, S. (2016). Study design and body mass influence RAIs from camera trap studies: Evidence from the felidae. *Animal Conservation*, *19*(1), 35-45.

- A comprehensive literature review of felid camera trapping projects, aiming to investigate how body mass and study design influence relative abundance indices (RAIs). An increase in the number of camera stations was found to negatively influence RAIs. Authors however argue that this might be due to an increase in camera trap density when studies increased the number of cameras, rather than density staying constant and survey area increasing when camera traps were added.

Colyn, R. B., Radloff, F., & O'Riain, M. J. (2018). Camera trapping mammals in the scrubland's of the cape floristic kingdom—the importance of effort, spacing and trap placement. *Biodiversity and Conservation*, *27*(2), 503-520.

- 50 cameras were used to produce a paired grid of 2 km by 2 km such that selective elimination of camera traps could be used to test the effect of different spacing, effort, and trap placement on species inventory and richness surveys. The study was based in the Cape Floristic Kingdom, and was meant to work towards a standardized methodology for camera trapping within the region, but the results are applicable elsewhere. Results suggest that a combination of camera density, spacing, total survey effort, and spatial coverage that combine to produce acceptable species richness estimates. The need for spatial representation across all habitat types within the study area is also important. Combined with a need for closure, this will result in some minimum number of cameras to be placed that will ensure proper density, acceptable levels of survey effort, spatial representation, and maintenance of closure.

Palmer, M. S., Swanson, A., Kosmala, M., Arnold, T., & Packer, C. (2018). Evaluating relative abundance indices for terrestrial herbivores from large-scale camera trap surveys. *African Journal of Ecology, 56*(4), 791-803.

- A large-scale camera trap grid was deployed to evaluate the accuracy of relative abundance indices for terrestrial herbivores compared to aerial abundance surveys. Cameras were sub-sampled to evaluate the impact of study design. Increasing the number of camera traps deployed significantly reduced variation in estimates for almost all species.

O'Connor, K. M., Nathan, L. R., Liberati, M. R., Tingley, M. W., Vokoun, J. C., & Rittenhouse, T. A. (2017). Camera trap arrays improve detection probability of wildlife: Investigating study design considerations using an empirical dataset. *PloS One, 12*(4), e0175684.

- Camera trap arrays were set (with arrays consisting of five non-independent cameras within a small plot) to investigate how the use of arrays vs. single cameras, and how the size of camera arrays, can affect detection probabilities in the eastern United States. Perfect detectability within a sampling session was approached as camera number within an array increased towards 5 of the cameras being considered with selective additions of additional camera traps from the array used for analysis. How close to perfect detectability was achieved depended on the species, however. It was found that a single camera at a site works for common species, but for less common species the addition of even one extra camera can vastly improve detection probability. Results also underline that one camera left out for a long time is not equal to multiple cameras left out for shorter periods- increasing camera number is much more efficient at increasing detections.

Rovero, F., Zimmermann, F., Berzi, D., & Meek, P. (2013). “Which camera trap type and how many do I need?" A review of camera features and study designs for a range of wildlife research applications. *Hystrix, 24*(2).

- An important foundational paper for choosing cameras, deciding on quantity, and how to use them. However, amounts of cameras are only explicitly laid out for random encounter model studies: the developers of the model suggest at least 50 camera trap placements. However, for capture-recapture models, it does note that there should be enough cameras to potentially capture between ten and thirty individuals to cameras.

Sollmann, R., Gardner, B., & Belant, J. L. (2012). How does spatial study design influence density estimates from spatial capture-recapture models? *PloS One, 7*(4), e34575.

- In this study, data from a black bear hair snaring study was used to investigate how spatial arrangement and size of the trapping grid affects SECR models. Although the study was executed using hair snaring, it should be noted that the conclusions drawn can be extended to camera trapping as both are point samples that can be used to create SECR models. Selective elimination of stations from analysis was used to investigate the effect on density estimates. When trap spacing was increased, there was very little change in estimates- in fact, the reduced area model was found to differ more from the model derived from the full data set than results with increased trap spacing, suggesting that it may be more worthwhile to space traps wider to sample a larger area. In other words, it was found that SECR models are much more robust to a smaller number of camera stations than other density estimation methods.

Tobler, M. W., & Powell, G. V. (2013). Estimating jaguar densities with camera traps: Problems with current designs and recommendations for future studies. *Biological Conservation, 159*, 109-118.

- A literature review of all jaguar density studies was conducted, study designs and results were reviewed and extracted, and simulated data was used to evaluate the different designs and statistical models. Results suggest for acceptable results, 40-50 camera stations are the bare minimum.

Wearn, O., & Glover-Kapfer, P. (2017). Camera-trapping for conservation: A guide to best-practices. *WWF-UK: Woking, UK.*

- A best practices review document for cameras, and the only one found that explicitly lays out guidelines for the suggested number of camera traps to use for different types of studies. The document suggests less than 20 cameras is unfeasible for species richness surveys, with 50 locations being a better target. It also notes that there are no hard rules for surveys used to produce relative abundance index surveys, though an increase in sampling locations increases precision. Precision is noted to be much improved when sampling at least 20 locations, and it is best to have more than 50 locations. For capture-recapture models, it is suggested to expose at least 5-10 individuals to sampling, for a naïve recommendation of 40-120 cameras when the separate suggestion of placing 4 cameras per home range is taken into account. For random encounter modelling, it is generally recommended to sample at least 20 locations, with ideally more than 50. Recommendation for occupancy depend on detection probability: for species with detection probabilities of at least .8, species can be detected with 30 sites or slightly less, however many species will need 30-60 sites while rare low-density species with detection probabilities less that .1 will need at least 100 sites.

1.5 How many camera days?

Summary: Camera days are an often-used method to express total survey effort, and are the product of the number of cameras deployed and the number of days each was deployed for. Very little in the literature was found to frame recommendations for trapping effort in terms of camera days. For more guidance on total survey effort, review sections 1.4, How Many Camera Traps? and 1.12, Timing/Length of Survey. Necessary camera days can vary depending on study objective and region. A study in eastern China found that 931 camera days were necessary to detect 90% of their study sites resident species, while 8700 days would be necessary to detect all of them (Si et al., 2014). A study specifically on elusive felids in Borneo found that different species differed in the amount of time necessary for first detection, varying from 700- 2,800 days (Wearn et al., 2013). Both studies were for species inventories/richness methods. The numbers for both of these studies fell mostly well within the range of suggested camera trap days for species richness surveys laid out in Wearn & Glover-Kapfer's (2017) camera trapping best practices document, from 600-1500 trap days for most species.

Wearn & Glover-Kapfer (2017) also included suggestions for roughly how many camera days are necessary depending on study objective. Recommendations include both number of camera trap days per location as well as in total. In general, they recommend 30 camera trap days per site for every state variable estimation survey type, including all types of density estimation, species richness estimation, relative abundance index, and occupancy estimation surveys. However, number of trap days may need to be increased for both density surveys of low density predators and for occupancy estimates. For species richness estimation surveys, the authors suggest a range of 600-1500 when the recommended number of camera trap days per location are multiplied by their suggested number of camera traps. Relative abundance surveys are suggested to have a total of at least 2,000 camera trap days to account for the need for multiple captures. For capture-recapture models, a ballpark estimate of necessary camera trap days is 1200, however for hard-to-detect species 60 camera days per location may be necessary which translates to 3600 days. Random encounter models were given a minimum suggestion of 2000 nights for low density carnivores, with less needed for more common species. Occupancy surveys were also recommended to have in total at least 1200 camera trap days.

The suggestions of Wearn & Glover-Kapfer (2017) are really ballpark estimates, with factors such as animal density and detectability influencing the minimum number of camera trap days that will be necessary for any single study (Rovero et al., 2013). Knowledge of specific focal species' detectability as well as a power analysis will shed more light on a specific study's necessary logistics (Rovero et al., 2013).

Si, X., Kays, R., & Ding, P. (2014). How long is enough to detect terrestrial animals? estimating the minimum trapping effort on camera traps. *PeerJ, 2*, e374.

- A two-year camera trap data set from a small study plot in eastern China was used to investigate minimum trapping effort and the effect of adding more cameras to a study. Analysis indicates that 931 camera days would capture 90% of the resident species, while around 8700 days would be necessary to detect all of them.

Wearn, O., & Glover-Kapfer, P. (2017). Camera-trapping for conservation: A guide to best-practices. *WWF-UK: Woking, UK.*

- A best practices review document for cameras, it also includes recommendations for overall camera trap nights for surveys attempting to estimate different state variables. For species richness surveys, 30 nights per location is the recommended number, giving a range of 600-1500 when multiplied by their suggested number of camera traps. The same suggestion is given for trap nights at each sampling point for relative abundance indices, but with multiple captures needed for RAIs, it is suggested to have at least 2,000 trap nights for most species. 30 camera trap nights are suggested as the minimum for capture-recapture models of density, with upwards of 60 trap nights for relatively precise results for most species, meaning a ball-park suggestion for total trap nights is 1,200 nights, or 3,600 nights for hard to detect species. It is suggested for REM models to have at least 30 trap nights per location, suggesting at least 2,000 trap nights in total for carnivores but less for other more common species. Greater than 30 camera trap nights per location are suggested for occupancy surveys for most species, suggesting again at least 1,200 nights.

Wearn, O. R., Rowcliffe, J. M., Carbone, C., Bernard, H., & Ewers, R. M. (2013). Assessing the status of wild felids in a highly-disturbed commercial forest reserve in borneo and the implications for camera trap survey design. *PLoS One, 8*(11), e77598.

- Performed a camera trapping survey for all feline species in a forest in Borneo using a strictly random study design. 700-2,800 camera days were necessary to detect each feline species.

1.6 Placement

Summary: Placement of camera traps can be thought as having two meanings: Placement at the site level, as well as placement within a site. Placement requirements vary widely depending on what the goal of the camera trap survey that is being undertaken is. Much of the literature seems to be in agreement that concerning at the site level, cameras should be placed evenly and randomly (in a systematic random design, rather than a simple random design), with most suggestions specifying a grid with a randomized starting point (O'Brien & Kinnaird, 2011; Rovero et al., 2013; Wearn & Glover-Kapfer, 2017). Systematic random designs can also allow for a clustered systematic random setup and/or nesting of cameras (refer to 1.10, Spacing).

Camera placement within a site is also a big consideration when camera trapping, and a considerable amount of research on how it affects results has been done. What the literature suggests depends on the state variable of one's camera trapping study. The use of relative abundance indices, species inventories, and occupancy studies are widespread, but many studies have shown that a variety of factors such as on- or off-trail placement, placement at other micro-habitat sites such as fallen logs, placement on human-use roads, placement location with a home range, placement relative to direction of animal travel, and other habitat features can influence detections of species or demographics within a species (with preferential space use causing either avoidance or adherence to features like trails) (Anile & Devillard, 2016; Blake & Mosquera, 2014; Brassine & Parker, 2015; Colyn et al., 2018; Cusack et al., 2015; Di Bitetti et al., 2014; Harmsen et al., 2010; Kays et al. 2010; Kolowski & Forrester, 2017; Larrucea et al. 2007; Mann et al., 2017; McCoy & Steury, 2011; Negrões et al., 2010; Wearn et al., 2013). One of the most important influences was on- vs. off-trail/road cameras, with most predators found to utilize trails frequently and many herbivores found to avoid them. As such, many of the cited studies suggest incorporating both on- and off-trail/road cameras for relative abundance indices, species inventories, and occupancy studies. Population density surveys, however, that include individual identification don't have such constraints, and in fact it is recommended to optimize placement for target species; for large carnivores like cats, this includes attempting to use trails and/or roads (Blake & Mosquera, 2014; Cusack et al., 2015; Di Bitetti et al., 2014; Harmsen et al., 2010; Kays et al. 2010; Mann et al., 2017; Negrões et al., 2010; Wearn et al., 2013 Wearn & Glover-Kapfer, 2017). There is variation between species though, and a review of the literature for focus species should be conducted; there are studies suggesting that even within predators, preferential use of things like trails depends on species, habitat, interspecific interactions, and demographic (for example, affinity for trails may decrease in more open habitats) (Brassine & Parker, 2015; Larrucea et al. 2007; Wearn et al., 2013). For specific recommendations for estimation of different state variables, refer to the papers below, especially the review papers such as Wearn & Glover-Kapfer (2017).

Cameras are best placed at trunk-level for focus species- some studies have started placing cameras higher up on trees to prevent theft- but it has been shown that if cameras are not in line with an animal's mass there will be missed captures (Meek et al., 2016). Cameras should also be placed with a view perpendicular to the direction of animal movement so as to have the highest chance of the animal triggering the sensor and to reduce invasiveness (Gibeau & McTavish, 2009; Rovero et al., 2013).

Anile, S., & Devillard, S. (2016). Study design and body mass influence RAIs from camera trap studies: Evidence from the felidae. *Animal Conservation, 19*(1), 35-45.

➢ A comprehensive literature review of felid camera trapping projects, aiming to investigate how body mass and study design influence relative abundance indices (RAIs). Paired camera placement were found to not influence RAIs, however, non-random vs. systematic sampling was found to strongly affect them (non-random sampling was defined as a survey in which placement and design was optimized for a specific species while systematic sampling design and placement has no focal species).

Blake, J. G., & Mosquera, D. (2014). Camera trapping on and off trails in lowland forest of eastern ecuador: Does location matter? *Mastozoología Neotropical, 21*(1), 17-26.

➢ Cameras were placed on- and off- trail to investigate the effect on captures rates and species composition in lowland Ecuador. Cameras did not differ in capture rate or overall species composition on-trail versus off- cameras within either one of those two groups did however vary between locations, suggesting overall location caused more variation than whether or not cameras were on trails. However, some species did show preferences for either of the two categories. Jaguars were captured only on trails (although there was a low sample size). Trail use in jaguars seems to vary between studies, suggesting potential differences in study areas. This study also lends some support to a combination of on- and off-trail cameras were species composition surveys and relative abundance surveys.

Brassine, E., & Parker, D. (2015). Trapping elusive cats: Using intensive camera trapping to estimate the density of a rare african felid. *PloS One, 10*(12), e0142508.

➢ Cameras were placed in both a randomized grid framework and at pre-selected cheetah scent-marking posts. Once at the randomized sites however, cameras were preferentially

placed on game trails. Regardless, the randomized grid framework survey had capture rates too low to estimate density using a capture-recapture framework. Cheetahs live in open environments where game trail use is not necessitated and occur at extremely low densities as well. The survey using cameras placed at scent marking posts however generated enough captures of enough individuals to use a SECR model to estimate population density without too much uncertainty. Results suggest that for low-density carnivores and open environments, trail placements for density estimation studies may not be enough and even more preferential placement may be needed, using attractive features like marking posts.

Colyn, R. B., Radloff, F., & O'Riain, M. J. (2018). Camera trapping mammals in the scrubland's of the cape floristic kingdom—the importance of effort, spacing and trap placement. *Biodiversity and Conservation*, *27*(2), 503-520.

- 50 cameras were used to produce a paired grid of 2 km by 2 km such that selective elimination of camera traps could be used to test the effect of different spacing, effort, and trap placement. Pairs of camera traps included a 'restricted' camera trap that was placed at an attractive location up to 20 m from the original study design's GPS point, while the other (referred to as expansive) could be placed up to 120 m away. Results were found to have higher measures of species richness, independent sightings, and capture frequencies when the maximum offset was larger. Cameras placed on more established trails with more animal signs produced higher estimates of species richness and respective capture rates. Camera placement was found to influence false trigger rates, with significantly higher rates with the restrictive placements, suggesting when possible optimization of camera trap placement with respect to signs of animal activity and game trails can improve the study.

Cusack, J. J., Dickman, A. J., Rowcliffe, J. M., Carbone, C., Macdonald, D. W., & Coulson, T. (2015). Random versus game trail-based camera trap placement strategy for monitoring terrestrial mammal communities. *PloS One, 10*(5), e0126373.

- To investigate the effect of camera placement on trails vs. off-trails, the terrestrial mammal community was surveyed in a park in Tanzania using two spatially and temporally concurrent surveys, the only difference being one utilized cameras placed on trails and the other utilized random placement. Richness, composition, and structure were compared. Significant differences did exist, but were found to be larger during the wet season and/or when low levels of sampling effort were used. Carnivores were found to prefer trails during the dry season, while large herbivores were found to prefer them during the wet season. Results showed however that a minimum sampling effort of 1400 camera trap nights was able to make placement strategy negligible for community survey results. However, the differences in capture probability do have to be taken in to account for other more taxon-specific surveys that look to estimate things like state variables.

Di Bitetti, M. S., Paviolo, A., & De Angelo, C. (2014). Camera trap photographic rates on roads vs. off roads: Location does matter. *Mastozoología Neotropical, 21*(1), 37-46.

- The effect of camera traps placed on roads vs. off roads on capture probabilities was investigated in the Atlantic Forest of Argentina. Species' capture probabilities differed significantly between the two placements, and species richness was found to be significantly higher on roads. The results once again suggest that differing trail or road use does bias detections, richness surveys, and the use of relative abundance indices. The authors suggest a combination of on- and off-trail/road cameras for species inventory surveys as well as surveys planning on using relative abundance indices.

Gregory, T., Carrasco Rueda, F., Deichmann, J., Kolowski, J., & Alonso, A. (2014). Arboreal camera trapping: Taking a proven method to new heights. *Methods in Ecology and Evolution*, *5*(5), 443-451.

- Arboreal camera trapping is a relatively underutilized and novel camera trapping approach. Up to publishing of this paper, only a handful of studies had used arboreal camera trapping, and all of them were characterized by extremely low camera number, low height in the canopy, and relatively low trapping effort. 25 cameras were used to monitor 13 natural bridges (tree bridges) created by the clearing of a pipeline right of way. Authors suggest placing cameras on the largest branches and closest to the trunk as possible to reduce movement caused by wind. The study did indicate that arboreal camera traps can produce significantly higher frequencies of false triggers most likely due to direct sunlight and higher wind. After leaf removal directly around the camera site, however, false triggers dropped quite a bit. Attempting to place cameras in clearings between leafy branches could work as well.

Gibeau, M., & McTavish, C. (2009). Not-So-Candid cameras: How to prevent camera traps from skewing animal behaviour.*3*, 35-37.

- Camera traps were found to cause wolves to react negatively to them while taking photos. The phenomenon has the ability to skew animal captures- for example, the wolf traveling at the head of the pack would react to the camera trap, and the rest of the pack would scatter, resulting in only partial captures of the other wolves or none at all. It was thought to be mostly due to white flashes, so choice of flash should play a role in reducing negative reactions, but the others suggest camera placement is important as well. The authors recommend to place cameras such that they are perpendicular to direction of travel whenever possible (reactions to camera traps were found to be most pronounced when they were coming head-on), and to use low-impact sites, not important microhabitats such as dens or salt-licks, to avoid affecting the study species.

Harmsen, B. J., Foster, R. J., Silver, S., Ostro, L., & Doncaster, C. P. (2010). Differential use of trails by forest mammals and the implications for camera-trap studies: A case study from belize. *Biotropica, 42*(1), 126-133.

- Investigated the use of trails by forest mammals and its effect on relative abundance indices by placing cameras both on and off trail in tropical forest in Belize. Jaguars and pumas were found to exhibit significant differences in trail use even though the two species have very similar niches. Different prey species also exhibited different levels of trail use or avoidance. Using cameras placed only on trails will thus bias species captures and skew relative abundance indices.

Kays, R., Tilak, S., Kranstauber, B., Jansen, P. A., Carbone, C., Rowcliffe, M. J., He, Z. (2010). Monitoring wild animal communities with arrays of motion sensitive camera traps. *arXiv Preprint arXiv:1009.5718.*

- Overview paper on the use of camera traps as integrated networks for monitoring (early paper). Cameras were use to monitor the animal community on Barro Colorado Island, Panama. When cameras placed on hiking trails (n=76) were evaluated vs. those placed in random locations within the forest (n=905), a significant different between trails and trap

rates for several species was found. Ocelots, the largest predator on the island were found to favour trails like many other carnivores have been found to, while some herbivores avoided them.

Kolowski, J. M., & Forrester, T. D. (2017). Camera trap placement and the potential for bias due to trails and other features. *PloS One, 12*(10), e0186679.

- 54 cameras were deployed at either log features or on trails, and then a paired camera was placed nearby randomly to study the affect of microhabitat choice and trail use on capture probabilities. Placement in general was found to affect the rate of species detections, total number of species detected, and detection probability. Species richness measures were also effected, as accumulation curves had steeper slopes on trails and logs than controls. More than 650 camera nights were estimated to be needed to remove the bias. RAIs were biased with features as capture rates increased. Some species were only photographed on logs. Even three of the five most commonly detected animals showed significantly different capture rates between controls and cameras with features. Detection probability varied not only in the more obvious of ways (deer commonly used game trails they themselves had made), but also in that even small rodents had higher detection probability on trails likely due to sight lines. In general, detection also varied with the size of either the trail or the log. One thing to note is that bears were found to not have differing detection probabilities; the authors posit that it may be due to their omnivorous diet meaning they have no need for efficient travel.

Larrucea, E. S., Brussard, P. F., Jaeger, M. M., & Barrett, R. H. (2007). Cameras, coyotes, and the assumption of equal detectability. *The Journal of Wildlife Management, 71*(5), 1682-1689.

- Used a marked, radio-collared population of coyotes to evaluate temporal and spatial factors on capture rates using camera traps with preferential placement on roads and trails. Placement was found to have a noticeable impact on capture rates, but with varying effects depending on the demographics- sites with higher human activity, such as old hunting shacks and dirt roads, actually had higher capture rates overall. However, pups were notably underrepresented at those sites, and much more likely to be captured far away from human-use areas. Where cameras were placed in relation to home territories (information gleaned from radio collars) also mattered; on territory edges, better representative samples of the population were captured as not only pack members were seen but transients and dispersers as well.

Mann, G. K., O'Riain, M. J., & Parker, D. M. (2015). The road less travelled: Assessing variation in mammal detection probabilities with camera traps in a semi-arid biodiversity hotspot. *Biodiversity and Conservation, 24*(3), 531-545.

- The effects of roads on detection probabilities of medium and large mammals in three vegetation types in the Little Karoo, an arid biodiversity hot spot in South Africa, were studied. The effect of three different vegetation types (fynbos, subtropical thicket, and riverine vegetation) were investigated. Vegetation types differed not only in composition but markedly in structure, with different thicknesses and densities. Each type had three survey transects, and efforts were made to reduce other factors in capture rates such as steep slopes. All roads were seldom used and unpaved. Number of mammal species varied markedly between vegetation types. Results suggest RAIs from data only on roads was unlikely to be representative of the mammal community. Data was analyzed at both the species level and feeding guild level, and animals at both levels differed in their usage of roads. Carnivores and insectivores were associated with roads, but herbivores and omnivores exhibited no significant relationship. The largest predators, caracals and leopards, had notably significant positive relationships with roads, whereas small predators such as mongooses had weak, non-significant positive relationships with distance from roads. With different affinities for roads, any studies that use capture frequencies to not only produce capture-recapture models of large cats but also estimate prey density with RAIs (a common occurrence) doesn't actually produce a meaningful result. Should be noted that other studies have exhibited avoidance of trails and roads by prey, but this may be because distances from roads for cameras were much smaller than in other studies due to changes in vegetation type that would have happened if distance from roads were increased. The authors suggest studies should use a mixed sign of cameras located on and off roads and trails.

Mccoy, J. C., Ditchkoff, S. S., & Steury, T. D. (2011). Bias associated with baited camera sites for assessing population characteristics of deer. *The Journal of Wildlife Management, 75*(2), 472-477.

- Compared cameras placed randomly, along trails, and at feed stations to assess the treatment's influences on relative abundances. Adult and yearling female captures at feed stations were similar to captures at randomly-placed cameras, but the rest of the age and sex classes that included fawns, yearling males, and adult males had much different capture rates when compared between sites. Trail-based cameras and random cameras had very similar capture rates, and exhibited capture ratios among sex and age classes that were also very similar, suggesting that trail-placed cameras will not skew estimates

of population parameters, at least with white-tailed tail. Results suggest trail-based placement vs. a random placement may not matter for at least white-tailed deer.

Meek, P. D., Ballard, G. A., & Falzon, G. (2016). The higher you go the less you will know: Placing camera traps high to avoid theft will affect detection. *Remote Sensing in Ecology and Conservation, 2*(4), 204-211.

- Placed cameras at 3 m and .9 m in height to quantify the difference in captures when cameras are placed at roughly the shoulder height of many mammal target species vs. higher up (a way to attempt to reduce theft). Captures were found to be dramatically lower for the cameras placed at 3 m above the ground, and suggests that camera lines of sight should be in line with an animal's trunk.

Negrões, N., Sarmento, P., Cruz, J., Eira, C., Revilla, E., Fonseca, C., Jácomo, A. T. (2010). Use of camera-trapping to estimate puma density and influencing factors in central Brazil. *The Journal of Wildlife Management, 74*(6), 1195-1203.

- Camera traps were used to estimate cougar abundance and occupancy over a three year period in central Brazil. Cameras were placed preferentially at different sites, including low- and high-use human roads and game trails. Pumas had higher calculated RAIs on roads compared to game trails, which affected overall results and demonstrates that even with preferential placement, not all sites are equal when it comes to influences on detectability.

Nichols, M., Glen, A. S., Garvey, P., & Ross, J. (2017). A comparison of horizontal versus vertical camera placement to detect feral cats and mustelids. *New Zealand Journal of Ecology, 41*(1), 145-150.

- The relative effectiveness of horizontal vs. vertical camera placement (horizontal meaning a traditional camera placement perpendicular to the ground, and vertical meaning looking down directly at the ground to standardize the amount of area captured) was investigated. 20 pairs of cameras (one horizontal and one vertical) were deployed to determine optimal alignment for invasive cats and mustelids (medium-sized predators). Captures of target species non-target species as well as false triggers were compared. Horizontal cameras captured 1.5 times as many images of the target species, detected more non-target animals, and did not significantly effect the number of false triggers.

Rovero, F., Zimmermann, F., Berzi, D., & Meek, P. (2013). "Which camera trap type and how many do I need?" A review of camera features and study designs for a range of wildlife research applications. *Hystrix, 24*(2).

- A foundational overview paper. Camera trap placement considerations are laid out by what state variable is of interest to the study. For faunal detection and inventories, there are technically no hard requirements. Single cameras should be placed throughout the study area, and camera placement can be opportunistic as there are no assumption to violate, but can also be random. For occupancy, cameras should be passive and random. Placement should also cover all habitat types of interest, and it is easiest if the placement of camera traps within each of those habitat types is proportional to the ratio of habitats. Absolute abundance or density surveys such as closed mark-recapture that utilize individual identification are suggested to be placed in pairs such that identification is more likely. Cameras can be placed opportunistically on game trails. For absolute abundance or density surveys that don't require individual identification such as the random encounter model, cameras must be placed randomly.

Taylor, B. D., Goldingay, R. L., & Lindsay, J. M. (2014). Horizontal or vertical? Camera trap orientations and recording modes for detecting potoroos, bandicoots and pademelons. *Australian Mammalogy, 36*(1), 60-66.

- The study investigated relative effectiveness of horizontal vs. vertical camera placement (horizontal meaning a traditional camera placement perpendicular to the ground, and vertical meaning looking down directly at the ground to standardize the amount of area captured). Each survey station (out of 21) consisted of three of the same brand of cameras directed at a bait container, with two cameras placed horizontally (one taking photos and the other videos) and one vertical camera taking photos. Target species were three medium-sized Australian mammals. Found that detection probability was lowest for the vertical camera for all three focus taxa and comparable for both horizontal cameras types. Other studies found that for medium- and small-sized mammals that vertical placement may be better for capture rates, however this study suggests otherwise.

Wearn, O. R., Rowcliffe, J. M., Carbone, C., Bernard, H., & Ewers, R. M. (2013). Assessing the status of wild felids in a highly-disturbed commercial forest reserve in borneo and the implications for camera trap survey design. *PLoS One, 8*(11), e77598.

- Performed a camera trapping survey for all feline species in a forest in Borneo using a strictly random study design. Comparing their results to previous studies, inter- and intra-specific differences in distribution of space use and habitat feature use that may influence the use of relative abundance indices were found. Like other studies, trail use was also found to differ wildly between species. Most importantly, estimates of relative abundance varied markedly between their survey and previous surveys, with previous surveys employing a biased sampling method. Clouded leopards had marked sexual differences:

males were often captured on logging roads, while females seemed to avoid them. By using both on and off trail cameras when trapping felids, it is suggested that it may result in more accurate abundance estimates. Above all, the study suggests random placement except for when using mark-recapture surveys.

1.7 Sampling units

Summary: There is very little literature exploring sampling unit considerations in the literature from the last ten years. What exists focuses on occupancy studies, perhaps because occupancy metrics were first theorized for discrete habitat areas such as ponds (Steenweg et al., 2018). Additionally, it may be that sampling units in terms of occupancy were explored more in-depth prior to 2010. Inter-trap spacing is what defines the sampling unit for occupancy studies, as such refer to section 1.10, Spacing Between Cameras. In general, consideration of a sampling unit seems that it should be important for some state variable estimations, as camera traps at their most basic are point samples, but often thought to be sampling some area around the camera. However, there is a dearth of literature on the subject.

Steenweg, R., Hebblewhite, M., Whittington, J., Lukacs, P., & McKelvey, K. (2018). Sampling scales define occupancy and underlying occupancy–abundance relationships in animals. *Ecology, 99*(1), 172-183.

- Includes a theoretical overview of occupancy as well as simulates point-location data within a SECR framework and then a test of the conclusions with camera trapping data to investigate further. Outlines that for areal sampling, the grid-cell size determines the size of the sampling unit, while for point sampling it determines the distance between sampling locations.

Wearn, O., & Glover-Kapfer, P. (2017). Camera-trapping for conservation: A guide to best-practices. *WWF-UK: Woking, UK.*

- A best practices review document, the only reference to sampling units is a note that when camera trapping to produce occupancy estimates, camera traps can be considered as either point samples or areal samples of some cell around the camera.

1.8 Attractants vs. no attractants

Summary: Attractants (including baits and scent, visual, and auditory lures) appear to still be slightly contentious within the literature, with there being no definitive agreements about their use. Multiple studies have shown that lures can be beneficial in several different ways, from increasing overall detections, improving likelihood of individual identification, increasing recapture rates (and thus precision in population estimates), decreasing time to first capture (and thus potentially allowing rotation of cameras either faster or at all), and increasing representation of camera-shy demographics (Brassine & Parker, 2015; Cove et al., 2014; Ferreras et al., 2018; Garrote et al., 2012; Gerber et al., 2012; du Preez et al., 2014). Some studies have also suggested that fears about unwanted influences on home ranges, animal movement rates, and immigration (that could influence population estimates) are unfounded, with none of the studies reviewed suggesting that any of those attributes were influenced (Braczkowski et al., 2016; Gerber et al., 2012; du Preez et al., 2014). However, other studies and one meta-analysis found that attractants had no effect at all on their studies (Anile & Devillard, 2016; Braczkowski, 2016; Stokeld et al., 2016), and one study found that bait stations exhibited relative abundances and demographics very different to that of non-baited camera trap stations (McCoy & Steury, 2011). These results overall though suggest that attractants can be a useful tool for the reasons previously mentioned, but only for abundance and density surveys, as well as species inventories, as the potential for lures or baits to influence capture rates will skew relative abundance indices, occupancy models, and potentially behavioural surveys (something unwanted for those survey types but positive for density/abundance surveys and species inventories).There does seem to be some variation in effectiveness by taxon, however, and some taxonomic groups such as mustelids were unrepresented in the literature review, so the effect on the focus species should be further thought upon and investigated before performing surveys.

Anile, S., & Devillard, S. (2016). Study design and body mass influence RAIs from camera trap studies: Evidence from the felidae. *Animal Conservation, 19*(1), 35-45.

- Performed a comprehensive literature review of felid camera trapping projects, resulting in 319 records from 53 countries, to investigate how body mass and study design affects relative abundance indexes (RAIs). Used generalized linear mixed models to account for repeat observations. Among other findings, found that the use of baits or lures in studies, which accounted for 30/319 records (7.7% of records), did not significantly influence relative abundance indices.

Balme, G., Hunter, L., & Robinson, H. (2014). Baited camera-trap surveys–Marginally more precise but at what cost? A response to du preez et al.(2014). *Biological Conservation,* (179), 144-145.

- Put forward several critiques concerning du Preez et al. (2014; see paper below). Notably, the paper didn't compare their density estimates against an independent estimate of population density, or even against a reference population, posing the question of whether the baited surveys were truly more accurate. They acknowledge baiting did increase the precision of the leopard population estimates, but the increase was incredibly small, potentially negating the substantial increase in man-hours for baited surveys. du Preez et al. (2014) also did not investigate whether their baiting violated closure assumptions- their attempt to use collared leopard's data on home range size during the period did not assess home range fidelity, investigate recapture differences when compared between surveys, or demonstrate how the home ranges of the collared leopards related to the sampling grid. Furthermore, there are worries about habituation to baits, which is a problem where leopards are trophy hunted using bait. This study outlines several

potential problems with du Preez et al.'s study, and suggests some critiques to keep in mind with other papers investigating the effect of attractants on camera trapping studies.

Braczkowski, A. R., Balme, G. A., Dickman, A., Fattebert, J., Johnson, P., Dickerson, T., Hunter, L. (2016). Scent lure effect on camera-trap based leopard density estimates. *PloS One, 11*(4), e0151033.

- Conducted two back-to-back camera trap studies using the same grid, the first study being a control with no scent lures deployed and the second being a 'treatment survey' with deployed scent lures. Study took place in a game reserve in South Africa. Both studies last forty days. Performed closed capture-recapture analysis as well as two spatially-explicit capture-recapture approaches. Closure tests suggested there was no breach of geographic closure. The lures did not have a significant effect on distances moved by the leopards, timing of leopard captures, nor number of captures. While the authors noted that leopards were thought to be relatively abundant within the reserve, they argue that lures in at least respectably dense predator habitat may not be necessary and that not using them may allow the avoidance of any bias not captured in this study.

Brassine, E., & Parker, D. (2015). Trapping elusive cats: Using intensive camera trapping to estimate the density of a rare african felid. *PloS One, 10*(12), e0142508.

- Cameras were placed in both a randomized grid framework and at pre-selected cheetah scent-marking posts. Once at the randomized sites however, cameras were preferentially placed on game trails. Regardless, the randomized grid framework survey had capture rates too low to estimate density using a capture-recapture framework- cheetahs live in open environments where game trail use is not necessitated and occur at extremely low

densities as well. By using the data collected from the pre-selected cheetah scent-marking posts, which are analogous to using scent lures, enough individuals were captured to use a SECR model to estimate population density without too much uncertainty. However, it should be noted that the original survey length of 30 days was insufficient, so the survey was extended to 90 days. When studying large felids, 90 days is the maximum recommended survey length to avoid violation of closure, though others have advocated for extending survey length to increase captures. However, there were no new captures during the extended survey, just recaptures, suggesting that even for low density populations 90 days is sufficient when using scented locations.

Cove, M. V., Spinola, R. M., Jackson, V. L., & Saenz, J. (2014). Camera trapping ocelots: An evaluation of felid attractants. *Hystrix, 25*(2)

- Investigated the effect of a visual lure (hung floppy discs) vs. two olfactory lures (cologne vs. sardines in oil) on camera trapping captures of ocelots. All three methods increased capture rates, although the visual lure had higher model support (though detection probabilities for all three had overlapping confidence intervals). The visual lure makes sense in that ocelots are primarily visual predators, which suggests that when baiting, one should take into account what type of predator the target species is.

Ferreras, P., Díaz-Ruiz, F., & Monterroso, P. (2018). Improving mesocarnivore detectability with lures in camera-trapping studies. *Wildlife Research, 45*(6), 505-517.

- The effects of two scent lures, when separate and mixed, and a non-reward bait on detection probability of Spanish mesocarnivores was investigated. Effectiveness of each varied depending on the species, but all attractants increased detection probability of at least one species. Similarly, all attractants were found to decrease the amount of days to

first detection, potentially allowing cameras to be rotated to different sites faster for larger coverage.

Garrote, G., Gil-Sánchez, J. M., McCain, E. B., de Lillo, S., Tellería, J. L., & Simón, M. Á. (2012). The effect of attractant lures in camera trapping: A case study of population estimates for the iberian lynx (lynx pardinus). *European Journal of Wildlife Research, 58*(5), 881-884.

- A camera grid was deployed that had alternating stations with and without lures to investigate their effect on detection rates and density estimations. At site locations, cameras were placed opportunistically along game trails and live pigeons in cages were used (no reward) to act as lures. Independent captures were almost equal between the two treatments, but many more photographs were taken at bait stations, as the bait seemed to get the lynxes to stick around such that the chance of capturing an identifiable photo was much higher. It should also be noted that 10 lynxes were known to inhabit the area- five of those being captured at non-baited stations and 9 at the baited stations. Capture probability at lure stations was thus higher than at the control treatments, and the estimates obtained with the blind cameras underestimated the number of lynxes compared to lured cameras. Results suggest proper lures can increase accuracy of CR analysis.

Gerber, B. D., Karpanty, S. M., & Kelly, M. J. (2012). Evaluating the potential biases in carnivore capture–recapture studies associated with the use of lure and varying density estimation techniques using photographic-sampling data of the malagasy civet. *Population Ecology, 54*(1), 43-54.

- Performed a camera trap study on Malagasy civets, a medium-sized predator, where half of the sampling duration was performed without a lure and the latter half of the sampling duration used chicken in a cage as a lure. Used three closure tests to investigate whether the lure caused breaches of closure; none suggested the assumption of closure had been violated. The use of lure did not alter abundance or density estimates, regardless of which of four density estimations they used. Also found no change in movement distances or temporal activity. However, lure did increase recaptures which helped to produce more precise population estimates.

Hofmeester, T. R., Cromsigt, J. P., Odden, J., Andrén, H., Kindberg, J., & Linnell, J. D. (2019). Framing pictures: A conceptual framework to identify and correct for biases in detection probability of camera traps enabling multi-species comparison. *Ecology and Evolution.*

- An overview paper of biases in detection probabilities, it notes that the use of attractant might violate the assumptions of some models such as the random encounter model, or occupancy models. If using a model in which bait does not violate any assumptions, it is noted that one should do their best to attempt to account for the use of bait in their statistical framework.

Larrucea, E. S., Brussard, P. F., Jaeger, M. M., & Barrett, R. H. (2007). Cameras, coyotes, and the assumption of equal detectability. *The Journal of Wildlife Management, 71*(5), 1682-1689.

- Used a marked, radio-collared population of coyotes to evaluate temporal and spatial factors on capture rates. Placement was preferential (cameras being placed on trails, roads, etc.) and 8, 6-week surveys were conducted. During the last survey, half of the cameras were scented. Scent was found to not influence detection rates. In addition,

scented cameras generally photographed coyotes at poor angles as their noses were almost always pointed at the scent. Attractant placement is thus always important to keep in mind.

du Preez, B., Loveridge, A. J., & Macdonald, D. W. (2014). Making the best of camera-trap surveys in an imperfect world: A reply to balme et al. *Biological Conservation*, (179), 146-147.

- Produced several points in response to Balme et al.'s 2014 response to du Preez et al. (2014; see above and below respectively). The authors note that big cats are wide-ranging animals that occur at low densities, and thus the biggest concern in population state variable surveys are low captures rates. They note they recorded 645 independent detections over 50 days with bait compared to 111 detections over the same length of time with no bait. This suggests for large felids worldwide it may be worth the effort to use attractants. They also reply that realistically a baseline population estimates requires costly long-term research which most scientists don't have the resources for, and their study only aimed to compare the efficiency of concurrent baited and unbaited surveys. Another pro that they argue shouldn't be ignored is that the use of their attractant allowed for positioning of the camera such that the angle of photographs were standardized for identification and sexing. Finally, any ethical concerns about habituation of bait in their study area was unfounded- leopard hunters already use bait.

du Preez, B. D., Loveridge, A. J., & Macdonald, D. W. (2014). To bait or not to bait: A comparison of camera-trapping methods for estimating leopard panthera pardus density. *Biological Conservation*, *176*, 153-161.

- Conducted two non-concurrent camera trap studies, one baited and one not, on African leopards in two regions of a national park in Tanzania. Surveyed in both studies for fifty days, using non-random placement. Some leopards were also collared to estimate home ranges and movement before and during the surveys. Data was analyzed using closed spatially-explicit capture-recapture models. Both the number of captures and the number of individuals were found to be significantly higher in baited surveys than unbaited surveys. Additionally, cubs (known often to be camera-shy) were only detected by baited traps. The addition of bait thus improved data quality and increased confidence in the density estimates. There was no significant difference in size or location of home ranges during the survey before, suggesting that the bait didn't attract animals from outside of the survey area to skew density calculations, either.

Mccoy, J. C., Ditchkoff, S. S., & Steury, T. D. (2011). Bias associated with baited camera sites for assessing population characteristics of deer. *The Journal of Wildlife Management, 75*(2), 472-477.

- Compared cameras placed randomly, along trails, and at feed stations to assess the treatment's influences on relative abundances. In total, 75% of deer photographed were at feeder stations, but percentage of photos from feed stations differed when broken up into different time intervals for pre-rut, rut, and post-rut. Adult and yearling female captures at feed stations were similar to captures at randomly-placed cameras, but the rest of the age and sex classes that included fawns, yearling males, and adult males had much different capture rates when compared between sites. Trail-based cameras and random cameras had very similar capture rates, and exhibited capture ratios among sex and age classes that were also very similar, suggesting that trail-placed cameras will not skew estimates of population parameters, at least with white-tailed tail. However, feed station cameras differed remarkably from both other placements, suggesting that attractants via feed cannot be used for anything other than to confirm presence of a species at a site.

Stokeld, D., Frank, A. S., Hill, B., Choy, J. L., Mahney, T., Stevens, A., Gillespie, G. R. (2016). Multiple cameras required to reliably detect feral cats in northern australian tropical savannah: An evaluation of sampling design when using camera traps. *Wildlife Research, 42*(8), 642-649.

- Assessed the influence of micro-habitat placement choices as well as the effects of three different lure types on feral cat detections in northern Australia. None of the lure types were found to influence detection rates, however it is noted that none of the captures showed the felines interested in any of the lures, suggesting that it may have been due to just the selection of lures (although the lures suggested had been used because they had previously shown results with feral cats elsewhere in Australia). The paper shows that lures aren't always effective, even when used properly so as to not bias captures.

1.9 Effects of invasiveness of camera traps on study objectives (CTs aren't truly non-invasive)

Summary: Camera traps, although notably less invasive than other more intensive study methods, are not completely non-invasive. Several studies have found that animals either react to cameras while being photographed (acting either attracted or repulsed) or avoid them completely (Gibeau & McTavish, 2009; Larrucea et al., 2007; Meek et al., 2016; Meek et al., 2014; Schipper, 2007). Gibeau & McTavish (2009) suggest ways to reduce this, such as ensuring cameras are placed perpendicular to direction of travel and avoiding the use of white flash, as do other overview papers reviewed above. These reactions and avoidance measures could potentially be a source of bias, most notably in behavioural and abundance/density surveys, and should be corrected for as much as possible.

Gibeau, M., & McTavish, C. (2009), Not-So-Candid cameras: How to prevent camera traps from skewing animal behaviour. *The Wildlife Professional, 3*, 35-37.

- Notes that in their studies on wolves in Banff National Park, wolves are often observed reacting negatively to camera traps taking photos. This skews captures as wolves travel in packs, and the first wolf generally sets of the camera, with the wolves following behind reacting to it before either fully in the frame or at all. This result influences can influence both behaviour studies as well as population counts. The authors note that the reactions are most pronounced when the flashes come from head-on, so suggest placing the camera perpendicular to the direction of travel. They also suggest against using cameras with white flashes, and advise against using high-impact sites for the target species (such as around dens, salt licks, etc.)

Larrucea, E. S., Brussard, P. F., Jaeger, M. M., & Barrett, R. H. (2007). Cameras, coyotes, and the assumption of equal detectability. *The Journal of Wildlife Management*, *71*(5), 1682-1689.

- Conducted a survey of marked and radio-collared coyotes to evaluate temporal and spatial factors on capture rates. Although the coyotes were known to be quite active during the day due to observations and GPS data, 83% of captures were recorded at night, significantly differing from their activity patterns. The authors suggest that it could be due to coyotes being very visual animals and may have had more trouble seeing the cameras at night. Suggests that animals may avoid cameras, which can bias detection rates.

Meek, P., Ballard, G., Fleming, P., & Falzon, G. (2016). Are we getting the full picture? animal responses to camera traps and implications for predator studies. *Ecology and Evolution*, *6*(10), 3216-3225.

- Conducted camera trap surveys for three years in eastern Australia. Used the captured photographs to evaluate behavioural responses of four mammal species to camera traps (cameras were unbaited). All four species reacted often to the traps, with individuals acting both attracted and repulsed by the traps, indicating that camera traps are not completely non-invasive as is the dominant thought for the technology. This has important impacts on behavioural studies and their conclusions, and suggests it is possible that behavioural responses could also bias detection probabilities.

Meek, P. D., Ballard, G., Fleming, P. J., Schaefer, M., Williams, W., & Falzon, G. (2014). Camera traps can be heard and seen by animals. *PloS One*, *9*(10), e110832.

- Conducted lab investigations to test the sound and light outputs of camera traps of 12 models, and compared the outputs to the hearing range of 12 mammal species and the vision ranges of 3 mammal species. Camera traps were found to produce sounds that are detectable within the range of most mammals' hearing and produced light that could be seen as well. The results suggest that this invasiveness should be considered when using camera traps.

Schipper, J. (2007). Camera-trap avoidance by kinkajous potos flavus: Rethinking the "non-invasive" paradigm. *Small Carnivore Conservation*, *36*, 38-41.

- In conducting a study using arboreal camera traps to study kinkajous, avoidance of the camera traps was observed. This may have been due to the noise or flash from the camera. Observations prior to setting the camera trap revealed a family of kinkajous crossing a branch that was considered a 'canopy highway' every couple of days, however after placement of the camera they were captured on the second night of the study and then not again for ten days. Observations of the site during the nights after the first captures showed the kinkajous avoiding the area directly in front of the camera, producing false negatives. Care should be taken to reduce this kind of avoidance to prevent negatively biasing detections.

1.10 Spacing between cameras

Summary: Inter-trap distance is an important consideration when designing camera trap studies, but requirements vary between study objectives, so considerable effort should be put into understanding constraints for the estimation of the state variable in question. Species inventories have no strict spacing requirements, though if captures will be used to estimate species richness, because of independence concerns it is often suggested to place cameras 1-2 kilometres apart (which is the general rule of thumb for practitioners to assume independence) (Colyn et al., 2018; Rovero et al., 2013;Wearn & Glover-Kapfer, 2017). The same suggestions hold true for surveys that use relative abundance indices, though when attempting to compare one's survey to others, spacing of one's study should be the same of that of the other study as an increase in inter-trap distance has been found to negatively correlate with RAIs (Anile & Devillard, 2016; Rovero et al., 2013;Wearn & Glover-Kapfer, 2017). For occupancy surveys, to be as useful and precise as possible it is suggested to space cameras at a home-range scale (that is, one home range diameter apart), in theory to ensure only one animal is recorded per sampling unit (Linden et al., 2017; Neilson et al., 2018; Rovero et al., 2014; Steenweg et al, 2018; Wearn & Glover-Kapfer, 2017). Capture-recapture models of density should have cameras placed at home-range scales or less; for SECR models optimum spacing is said to be .3 times home range diameter of the focal species, with up to .8 times the home range diameter being acceptable (O'Brien & Kinnaird, 2011; Rodríguez-Soto et al., 2010; Rovero et al., 2014; Wearn & Glover-Kapfer, 2017). Rovero et al. (2013) says that a common rule of thumb is to set two cameras per home range area. For random encounter models of density, the two review papers that cover the method differ: Rovero et al. (2013) state that cameras must simply be far enough apart to avoid sampling just one individual repeatedly such that independent records can be obtained, while

Wearn & Glover-Kapfer (2017) suggest that cameras should be spaced farther apart than home range diameter.

Some of these suggestions are general field practices, and some studies' results suggested practices that differ from those generally accepted by the community. A study by Kays et al. (2010) found that spatial autocorrelation between camera traps was not an issue when placed more than 25 metres apart, suggesting the rule of thumb of at least 1 kilometre apart to avoid autocorrelation is unnecessary. However, that study took place in tropical forest, while a study in subtropical scrub found that autocorrelation was still an issue at inter-trap distances of 500 metres (Colyn et al., 2018). In a related vein, a study of interactions between Tasmanian devils and domestic cats found avoidance over short distances, which could be a problem when surveying multiple species, or surveying for one species that might be exhibiting such an avoidance pattern (Fancourt, 2016). The potential for these issues should be considered when designing a study. There are also some indications in the literature that SECR models are more robust to increases in inter-trap distances past what is normally suggested, and that increasing spatial area is more important than preserving recommended camera trap density, so that it may be worthwhile to space camera traps further apart to sample a wider area (Sollmann et al., 2012; Zimmermann, 2013). One study tested a standardized trapping grid that was a compromise of a trapping grid for multiple sympatric carnivore species' ability to accurately estimate their densities, and found that by sacrificing a little precision much time and effort was saved by one deployment while still being able to produce reliable estimates (O'Brian & Kinnaird, 2011).

The above papers have dealt with spacing of independent cameras, but if logistical constraints allow it, papers that have studied the utility of placing multiple, non-independent cameras at a site either on the same tree/post or in close proximity to one another have also demonstrated that it can significantly increase detection probability of a species much more so than the most often used method of increasing the number of trapping nights, though it is less useful for common species (O'Connor et al., 2017; Pease & Holzmueller, 2016; Stokeld et al., 2016). An increase in detection probability has many benefits, including stronger statistical power and potential shorter survey lengths needed, such that survey costs can be cut.

Anile, S., & Devillard, S. (2016). Study design and body mass influence RAIs from camera trap studies: Evidence from the felidae. *Animal Conservation*, *19*(1), 35-45.

- A comprehensive literature review of felid camera trapping projects, aiming to investigate how body mass and study design influence relative abundance indices (RAIs). Analysis showed that inter-trap distance was negatively correlated with RAIs, suggesting that spacing should be taken into account when conducting surveys intended to produce relative abundance indices, and especially when attempting to compare RAIs between surveys.

Colyn, R. B., Radloff, F., & O'Riain, M. J. (2018). Camera trapping mammals in the scrubland's of the cape floristic kingdom—the importance of effort, spacing and trap placement. *Biodiversity and Conservation*, *27*(2), 503-520.

- A 2 kilometre by 2 kilometre grid of camera traps was set up in South African scrubland with cameras spaced every 500 metres (such that cameras could be selectively eliminated) to investigate the effect of spacing and trap placement on species richness estimates. The results suggest that reliable estimates of richness in subtropical scrubland work when cameras are spaced at least 1 kilometre apart from each other- 500 metres was found to cause issues with independence. The authors argue that a standardised protocol for all habitats and species is unrealistic, however they could be feasible for specific habitats and/or target species guilds.

Fancourt, B. A. (2016). Avoiding the subject: The implications of avoidance behaviour for detecting predators. *Behavioral Ecology and Sociobiology, 70*(9), 1535-1546.

- Camera traps were used to study two sympatric predators, the Tasmanian devil and the feral cat. Results found that devil and cat detections were negatively correlated, but it wasn't due to one predator suppressing the other- cats were found in analysis to avoid devils at short distances, suggesting that negative relationships in detections at a site may be due to avoidance and not suppression. This has wider implications for RAIs and abundance surveys. Cameras are often spaced far apart, however, previous research shows avoidance can be on a much smaller scale. This suggests cameras may have to be spaced closer together than thought if there is a potential for avoidance. How close cameras should be, or whether that would interfere with independence, was not investigated within the study.

Gálvez, N., Guillera-Arroita, G., Morgan, B. J., & Davies, Z. G. (2016). Cost-efficient effort allocation for camera-trap occupancy surveys of mammals. *Biological Conservation, 204*, 350-359.

- The study examines camera trap survey cost as a function of the number of sampling units, survey duration, and camera traps per sampling unit to investigate how best to optimize results while taking cost into account. Additionally, a dataset was used to investigate the deployment of multiple camera traps per sampling unit. Results suggest that one camera trap per sampling unit is fine for common species, but for more elusive species minimum survey costs can be achieved with multiple cameras per sampling unit

and fewer sampling locations. Multiple camera traps set within a single sampling unit were also found to be able to yield independent species detections.

Kays, R., Tilak, S., Kranstauber, B., Jansen, P. A., Carbone, C., Rowcliffe, M. J., He, Z. (2010). Monitoring wild animal communities with arrays of motion sensitive camera traps. *arXiv Preprint arXiv:1009.5718,*

- Overview paper on the use of camera traps as integrated networks for monitoring. Cameras were use to monitor the animal community on Barro Colorado Island, Panama. With cameras paired within plots, pairs were analyzed to investigate autocorrelation. Results indicate autocorrelation is not a problem at distances greater than 25 metres, meaning cameras may be able to be placed much closer than thought.

Linden, D. W., Fuller, A. K., Royle, J. A., & Hare, M. P. (2017). Examining the occupancy–density relationship for a low-density carnivore. *Journal of Applied Ecology, 54*(6), 2043-2052.

- Using a paired study of camera trap surveying and baited hair snares for fishers, the study was used to investigate whether occupancy is an appropriate approximation of density. Occupancy and Royle-Nichols models were fit to camera data and a SECR model was fit to snare data, and a close relationship between grid cell estimates of the state variables for the fishers from the two different types of data, suggesting that when spatial grain is the same or slightly below that of home range size for a focal species camera traps can give accurate measures of occupancy, related to density, that can be used as a proxy for management.

Neilson, E. W., Avgar, T., Burton, A. C., Broadley, K., & Boutin, S. (2018). Animal movement affects interpretation of occupancy models from camera-trap surveys of unmarked animals. *Ecosphere*, *9*(1).

- To investigate the effect of animal movement on occupancy metrics from camera traps, animal movement simulations were created that varied in movement rate, home range size, and population density. Camera trap sampling design was also varied in terms of duration of sampling and camera trap density for the models. Single-species occupancy models were then fit to the simulated data, and results were compared to the asymptotic proportion of area occupied. Varying the spacing of camera traps by an order of magnitude had very little impact on the accuracy of model estimates of detectability and occupancy, however the interpretation of the metric at such a different scale would change. However, especially when animals moved over large home ranges and camera trap spacing was small, subsequently increasing inter-trap distance lead to an improvement in estimates, suggesting that spacing camera traps at a scale that matches home range size does provide more accurate metrics while also making interpretation of occupancy easier.

O'Brien, T. G., & Kinnaird, M. F. (2011). Density estimation of sympatric carnivores using spatially explicit capture–recapture methods and standard trapping grid. *Ecological Applications, 21*(8), 2908-2916.

- The use of a standard trapping grid to produce capture-recapture density estimates of sympatric carnivore species in Africa was investigated, as often CR studies focus on one species and base spacing off of home range sizes of that species. Cameras were placed at distances of roughly 1.4 kilometres apart, on the closest game trail to the GPS point.

Results showed that above-average sample sizes of 18-26 individuals were obtained per species, without attempting to capture any species in particular. Coefficients of variation for density estimates were also comparable to those of other studies on each of the focus species that had a study design for just one focus animals. A little precision was shown to have been sacrificed, but the results indicate that standardized designs for multiple species coupled with not requiring multiple deployments for each species can yield great savings in cost and effort without an unreasonable amount of sacrifice.

O'Connor, K. M., Nathan, L. R., Liberati, M. R., Tingley, M. W., Vokoun, J. C., & Rittenhouse, T. A. (2017). Camera trap arrays improve detection probability of wildlife: Investigating study design considerations using an empirical dataset. *PloS One*, *12*(4), e0175684.

- Camera trap arrays were set (with arrays consisting of five non-independent cameras within a small plot) to investigate how the use of arrays vs. single cameras, and how the size of camera arrays, can affect detection probabilities in the eastern United States. Perfect detectability within a sampling session was approached as camera number within an array increased towards 5 of the cameras being considered with selective additions of additional camera traps from the array used for analysis. How close to perfect detectability was achieved depended on species however. It was found that a single camera at a site works for common species, but for less common species the addition of even one extra camera can vastly improve detection probability.

Pease, B. S., Nielsen, C. K., & Holzmueller, E. J. (2016). Single-camera trap survey designs miss detections: Impacts on estimates of occupancy and community metrics. *PloS One, 11*(11), e0166689.

- At 20 camera sites, four cameras were placed on one tree at right angles to one another for a detectability at 360 degrees. Total captures when one camera, two cameras, or four cameras from each site were pooled and then analyzed. The four-camera survey method detected 1.25 more species per site than the one-camera method, but it should be noted that one-camera trap surveys did detect all mammal species, suggesting for inventories that one camera per site can be enough. However, for the estimation of other state variables, higher detection probabilities are better, and increasing the number of cameras did increase detection probabilities. With more cameras at a site came increased detection probabilities and occupancy estimates more similar to the naive estimate. It was also found that no species-specific detection history generated the same best-fitting habitat model between one- and four-camera survey methods. This suggests that directional placement and number of cameras can greatly influence detection probabilities. The authors recommend including at least two cameras at every site to improve low detection rates.

Rodríguez-Soto, C., Urios, V., Monroy-Vilchis, O., Soria-Díaz, L., & Zarco-González, M. (2010). Variation of abundance and density of puma concolor in zones of high and low concentration of camera traps in central mexico. *Animal Biology*, *60*(4), 361-371.

- Camera traps were used to estimate the density and abundance of pumas in Central Mexico, while varying the density of camera traps to investigate the effect on their estimates. Densities were originally varied because home range size of pumas in Mexico was unknown. The low-density treatment had an inter-trap distance of 4.6 kilometres, less than the diameter of the minimum known home range for a female puma, and the high-density treatment had a spacing of 1.8 kilometres, less than the diameter of the minimum home range for a female jaguar. Puma densities were found to be slightly higher in the high-density camera trap treatment survey, but it was thought to be due to an increased probability of registering and recapturing pumas. The authors suggest separating camera traps by a distance of 3.2 kilometres, which was found to be the maximum distance moved of 8 pumas. Home range size was thus found to be very important information for study design, and the results suggest that inter-trap spacing for density surveys does indeed need to be at or below home range size.

Rovero, F., Zimmermann, F., Berzi, D., & Meek, P. (2013). "Which camera trap type and how many do I need?" A review of camera features and study designs for a range of wildlife research applications. *Hystrix, 24*(2)

- A best practices review document, the paper includes recommendations for spacing based on study objective, as recommendations vary based on what metric a study is aiming to estimate. For faunal detections and inventories, there are no requirements in terms of spacing, though even spacing within a grid allows for more rigorous analysis such as species accumulation curves. Occupancy analyses require that cameras are placed in a grid with distances between traps being larger than the diameter of an average home range for the species of interest to avoid spatial autocorrelation. For capture-mark-recapture models of density and abundance, there should be at least one camera per animal home range, and thus cameras should be spaced at most at the scale of home range, though a common rule of thumb is to set at least two cameras per minimum home range size of the target species. Random encounter modeling of abundance or density only requires that cameras should be spaced enough to avoid sampling the same individual repeatedly to obtain independent records.

Sollmann, R., Gardner, B., & Belant, J. L. (2012). How does spatial study design influence density estimates from spatial capture-recapture models? *PloS One, 7*(4), e34575.

- In this study, data from a black bear hair snaring study was used to investigate how spatial arrangement and size of the trapping grid affects SECR models. Although the study was executed using hair snaring, it should be noted that the conclusions drawn can be extended to camera trapping as both are point samples that can be used to create SECR models. Selective elimination of stations from analysis was used to investigate the effect on density estimates. When trap spacing was increased, there was very little change in estimates- in fact, the reduced area model was found to differ more from the model derived from the full data set than results with increased trap spacing, suggesting that it may be more worthwhile to space traps wider to sample a larger area. The study's simulations also suggest that SECR models are robust as long as mean animal movement was equal to at least half of the distance between traps.

Steenweg, R., Hebblewhite, M., Whittington, J., Lukacs, P., & McKelvey, K. (2018). Sampling scales define occupancy and underlying occupancy–abundance relationships in animals. *Ecology*, *99*(1), 172-183.

- Includes a theoretical overview of occupancy as well as simulating point-location data within a SECR framework and then a test of the conclusions with camera trapping data to investigate further. Sampling for occupancy estimates have no true requirements, but depending on the spacing of cameras, the interpretation of the data differs. Refer to the paper for an in-depth exploration of occupancy across scales, and how camera spacing changes that. Occupancy is one-to-one with abundance (and many aim to use occupancy as a proxy for abundance) with territorial animals when working at home-range scales-thus, placing cameras at home-range scales should be used when the goal of occupancy is to be used as a proxy for abundance. This can also be done for less territorial animals, but should be noted that the relationship between occupancy and abundance is curvilinear, and the curve for that species should be investigated. Camera traps can be used for estimating occupancy of multiple species, but it should be noted that the definition of occupancy for all the species captured will vary, depending on home range size and true density.

Stokeld, D., Frank, A. S., Hill, B., Choy, J. L., Mahney, T., Stevens, A., Gillespie, G. R. (2016). Multiple cameras required to reliably detect feral cats in northern australian tropical savanna: An evaluation of sampling design when using camera traps. *Wildlife Research, 42*(8), 642-649.

- The influence of three different lures and the use of multiple camera traps at a site on capturing feral cats was assessed in Australia. Micro-habitat placements included along discrete pathways through dense vegetation, dry creek beds or gullies, and open woodland with no discernible game trails. Cameras were angled between south-west and south-east to avoid false detections from the sun. Using five cameras at a site vs. using one camera was investigated, and detections increased 50% when using the multiple-camera array. The increased detection probabilities also increased precision of estimates.

Tobler, M. W., & Powell, G. V. (2013). Estimating jaguar densities with camera traps: Problems with current designs and recommendations for future studies. *Biological Conservation, 159*, 109-118.

- A literature review of all jaguar density studies was conducted, study designs and results were reviewed and extracted, and simulated data was used to evaluate the different designs and statistical models. Most studies were found to not meet the requirements that the simulations demonstrated were necessary: camera polygons should be at least the size of one home range, and spacing should be at most equal to the radius of a female home range (any larger and females can potentially not be counted; females having smaller range sizes). This spacing requirement should apply for all density/abundance estimation studies, and the simulation acts as evidence to support the recommendation, which can also be found in multiple camera trapping guides.

Wearn, O., & Glover-Kapfer, P. (2017). Camera-trapping for conservation: A guide to best-practices. *WWF-UK: Woking, UK.*

- A best practices review document, the paper contains recommendations for spacing when attempting to estimate all state variables, as recommendations differ based on objective. Recommendations include: Species inventories employ no formal models and because of that, no assumptions are explicitly made- because of that, there are no requirements for spacing, and with cameras often placed in targeted, non-random locations, the spacing can change to incorporate that. Species richness and diversity surveys should be independent, and in general for camera trap surveys practitioners use inter-trap distances of 1-2 kilometres, though there is not much empirical reasoning for it. The recommendation is the same for relative abundance indices, if trapping rate from each camera is to be treated as a data point within a statistical framework. For capture recapture models, SECR models are recommended to have cameras placed at distances of one third of a home-range radius for reasonably precise estimates, with a maximum of .8 times an average home range. For conventional capture-recapture, cameras must just be spaced apart by less than one home-range diameter. Random encounter modelling

depends on home range size as well- spacing should be larger than home-range size for focal species to ensure independence, but in the absence of home-range information 1-2 kilometres is recommended. Finally, occupancy studies should also space cameras one home-range diameter apart.

Zimmermann, F., Breitenmoser-Wursten, C., Molinari-Jobin, A., & Breitenmoser, U. (2013). Optimizing the size of the area surveyed for monitoring a eurasian lynx (lynx lynx) population in the swiss alps by means of photographic capture–recapture. *Integrative Zoology, 8*(3), 232-243.

- 5 nested plots of cameras that ranged in survey area from 65 to 760 kilometres squared were used to assess the effect of survey area size on non-spatial and spatial capture-recapture density estimations. The non-spatial CR model estimates decreased significantly from the smaller sample areas to the largest sample areas, while SECR models did also decrease but not significantly. The results suggest that SECR models are more robust, but regardless that large spatial efforts of greater than roughly 760 kilometres squared are needed to reliably estimate density for low-density carnivores. This should be taken into account when calculating inter-trap density.

1.11 Rotation of cameras to new sites

Summary: There is very little literature in the past ten years on rotating camera traps to new locations within a single study. This may be because the reasoning behind this common recommendation is purely theoretical (by moving camera traps around one can sample more microhabitats) or it may just be that the issue was explored more than ten years ago (the scope of this annotated bibliography). Rotating individual cameras to new sites within a single survey can only be recommended for species inventory and species richness surveys- in addition to being suggested by several review papers like Rovero et al. and Wearn and Glover-Kapfer (2013, 2017), a study by Si et al. (2014) showed quantitatively that moving cameras rather than leaving them in one place for longer is more a more efficient way to increase species detections. The other way it is possible to move cameras, in blocks, can be done with surveys attempting to estimate other state variables such as occupancy and density in order to increase the amount of area surveyed when the amount of camera traps available for the study are low.

Rovero, F., Zimmermann, F., Berzi, D., & Meek, P. (2013). "Which camera trap type and how many do I need?" A review of camera features and study designs for a range of wildlife research applications. *Hystrix, 24*(2).

- An important recommendations/foundational paper for choosing cameras, deciding on quantity, and how to use them. It suggests rotating individual cameras to new sites every 15 to 30 days for species inventories. For other surveys with different objectives, such as estimating occupancy or density, it is suggested to sample areas in blocks (moving all cameras at once to new blocks) when the total amount of available cameras to be used for a study is low so as to increase area covered.

Si, X., Kays, R., & Ding, P. (2014). How long is enough to detect terrestrial animals? estimating the minimum trapping effort on camera traps. *PeerJ, 2*, e374.

- A two-year camera trap data set from a small study plot in Eastern China was used to investigate minimum trapping effort and the effect of adding more cameras to a study. Analysis of the effect of adding new cameras suggests that rotating cameras to new sites, rather than leaving them at their original location, is a much more efficient way of increasing captures. The optimal sampling period for a site was found to be roughly 40 days.

Wearn, O., & Glover-Kapfer, P. (2017). Camera-trapping for conservation: A guide to best-practices. *WWF-UK: Woking, UK.*

- A best practices review document, the paper touches on rotation of cameras. It is suggested in general to rotate individual cameras to new locations ‘relatively frequently’ to maximise the number of different microhabitats sampled for species inventories and richness surveys. It also briefly mentions the ability to deploy cameras and sample areas in blocks, but does not recommend it per se.

1.12 Setting traps for one sampling objective vs. multiple

Summary: There is a relative lack of publications in the literature looking specifically at the effects of attempting to set traps for multiple objectives. Hofmeester et al. (2019), in attempting to lay out a conceptual framework to identify and correct for biases in detection probability linked to things like study design and camera placement, have given a way for practitioners to account for differences when attempting to sample multiple species to produce state variable estimations for each one. This, however, does also depend on which state variable one is attempting to estimate. For example, Steenweg et al. (2017), note that one grid can be used to estimate occupancy of multiple species, but because the definition of occupancy varies depending on sampling scale, the meaning of the metric for each species will be different. The most pertinent example to be found in the literature, O'Brien et al. (2011), investigated the use of a standard trapping grid to use SECR models to estimate the density of multiple carnivore species. It found that their captures were able to produce reasonable estimates without sacrificing too much precision, suggesting that for at least some study metrics, cameras can be set for multiple objectives to be more efficient with time and money while not sacrificing too much. Conversely however, Shannon et al. (2014), found that for species that weren't common, study design and placement for occupancy studies of different North American mammal species differed quite a bit, making it difficult for one survey to have high enough capture probabilities for multiple species. Overall, whether setting camera traps for multiple objectives is feasible seems to be highly variable depending on study metric(s) and species and should be considered before starting any study.

Hofmeester, T. R., Cromsigt, J. P., Odden, J., Andrén, H., Kindberg, J., & Linnell, J. D. (2019). Framing pictures: A conceptual framework to identify and correct for biases in detection probability of camera traps enabling multi-species comparison. *Ecology and Evolution.*

- A literature review was performed and author experience was used to compile factors that affect camera trap detections of animals, from which a conceptual framework was outlined that allows identification and correction for bias in detection probability. The framework allows for correction for most sources of bias, including different study designs, multiple species, etc., meaning that multiple sampling objectives should generally be feasible.

O'Brien, T. G., & Kinnaird, M. F. (2011). Density estimation of sympatric carnivores using spatially explicit capture–recapture methods and standard trapping grid. *Ecological Applications, 21*(8), 2908-2916.

- The use of a standard trapping grid to produce capture-recapture density estimates of sympatric carnivore species in Africa was investigated, as often CR studies focus on one species and base spacing off of the home range size of that species. Cameras were placed at distances of roughly 1.4 kilometres apart, on the closest game trail to the GPS point. Results showed that above-average sample sizes of 18-26 individuals were obtained per species, without attempting to capture any species in particular. Coefficients of variation for density estimates were also comparable to those of other studies on each of the focus species that had a study design for just one focus animals. A little precision was shown to have been sacrificed, but the results indicate that standardized designs for multiple species coupled with not requiring multiple deployments for each species can yield great savings in cost and effort without an unreasonable amount of sacrifice.

Shannon, G., Lewis, J. S., & Gerber, B. D. (2014). Recommended survey designs for occupancy modelling using motion-activated cameras: Insights from empirical wildlife data. *PeerJ, 2*, e532.

- To investigate the effect of survey design on the accuracy and precision of occupancy estimates, 40 cameras were placed across a 160 square kilometre grid. 54 different surveys designs were tested by selectively removing cameras from data analysis. Data was used to estimate detection probabilities and occupancy estimates, then those were used to create simulations to evaluate optimal survey design. Substantial differences in optimal study design were found depending on focal species, indicating that surveying as many sites as possible is not always the best approach. Differences in optimal survey design for different species mean that multi-species studies will have less precision, though they shouldn't be considered useless. Optimizing placement for a couple of species is an option among others such as using more than just camera traps for surveys.

Steenweg, R., Hebblewhite, M., Whittington, J., Lukacs, P., & McKelvey, K. (2018). Sampling scales define occupancy and underlying occupancy–abundance relationships in animals. *Ecology, 99*(1), 172-183.

- Includes a theoretical overview of occupancy as well as a simulation of point-location data within a SECR framework and then a test of the conclusions with camera trapping data to investigate further. In exploring the definition of occupancy, it's noted that the definition of occupancy changes with scale. Thus, detections of multiple species with different home ranges can all be used within occupancy frameworks, however the interpretation of the estimates will differ.

1.13 Timing/length of survey (for short-term studies/studies worried about closure)

Summary: Time in camera trap studies is an important consideration; this includes both the timing of study (i.e. at what point in the year it takes place) as well as for how long the study lasts. Recommendations for both of those considerations vary in the literature depending on the goal of the survey.

Time of year is an important consideration due to animal phenology. In the literature, time of year has been found to influence capture rates and associated metrics like relative abundance as well as occupancy and density estimates (Cusack et al., 2015; Larrucea et al., 2007; Weingarth et al., 2015; Wearn & Glover-Kapfer, 2017). This was due to demographic changes such as whelping and dispersal, in the case of Larrucea et al. (2007), or due to micro-habitat selection during different times of the year in the case of Cusack et al. (2015). These factors may not be issues for species inventories, where just a detection is required, but may be important for studies aiming to estimate occupancy, density, relative abundance, etc. where it's important to get a good sample size or where closure is an issue. Shannon et al. (2014) recommend that, at least for multi-species occupancy surveys, that biologically meaningful survey times may vary between species and it may be better to define a sampling period and then consider what can species can be meaningfully sampled within it.

Recommendations for the length of one's survey are similar. Unless one is aiming to capture the species richness or create a species inventory for just one season in a specific location, there are no restrictions in how long cameras can be set for in species richness or inventory surveys. However, most estimation methods for occupancy and density have assumptions of closure, for example 90 days being the rule of thumb for many carnivores for density studies (Brassine &

Parker, 2015). With an upper limit set, acceptable detectability becomes a question of how many cameras are set out and the corresponding number of camera days (see Sections 1.4 and 1.5, How Many Cameras? and How Many Camera Days?). The literature suggests that should not be too much of a problem, however. In general, it is often suggested to increase survey length to increase detections (Brassine & Parker, 2015; O'Connor et al., 2017; Shannon et al., 2014; Wearn & Glover-Kapfer, 2017). Basically, that one camera trap in the field for a long time is equal to multiple traps out in the field for less time. However, multiple studies show that increasing survey length is the least effective method to increase detectability and detections or decrease uncertainty, that better placement or increasing cameras is much more effective, and as such the risk of breaching closure by increasing survey length is not worth it (O'Connor et al., 2017; Rovero et al., 2013; Shannon et al., 2014). Rotation of cameras is another way for some study designs, such as species inventories, to reduce length (Si et al., 2014). This is furthermore bolstered by studies such as Brassine & Parker and Weingarth et al. (2014; 2015) that show that even for the low-density, elusive carnivores, proper placement and study design should ensure acceptable capture rates within 90 days.

Brassine, E., & Parker, D. (2015). Trapping elusive cats: Using intensive camera trapping to estimate the density of a rare african felid. *PloS One*, *10*(12), e0142508.

- Cameras were placed in both a randomized grid framework and at pre-selected cheetah scent-marking posts to investigate the effect of the placements on density estimates using a capture-recapture framework. The randomized grid framework had capture rates too low to estimate density, but the preferential placements at scent-marking posts did generate enough images. However, after 90 days (the maximum recommended amount of time for capture-recapture studies to maintain closure), cameras were left out in attempt to increase precision of density estimates. Density estimates were more precise, however only due to recaptures, not due to new captures, suggesting 90 days does suffice for the survey of the lowest of low-density predators such that closure can be maintained.

Cusack, J. J., Dickman, A. J., Rowcliffe, J. M., Carbone, C., Macdonald, D. W., & Coulson, T. (2015). Random versus game trail-based camera trap placement strategy for monitoring terrestrial mammal communities. *PloS One, 10*(5), e0126373.

- To investigate the effect of camera placement on trails vs. off-trails, the terrestrial mammal community was surveyed in a park in Tanzania using two spatially and temporally concurrent surveys, the only difference being one utilized cameras placed on trails and the other utilized random placement. Species richness, composition, and structure were compared. Time of year and length of survey both caused differences in captures; for example, carnivores varied their trail use during the year (preferring trails during the dry season) while large herbivores preferred them in the wet season. It was suggested that a minimum sampling effort of 1400 camera trap nights would be needed to make placement strategy negligible for community surveys, but that still would not even out differences due to time of year.

Larrucea, E. S., Brussard, P. F., Jaeger, M. M., & Barrett, R. H. (2007). Cameras, coyotes, and the assumption of equal detectability. *The Journal of Wildlife Management*, *71*(5), 1682-1689.

- Conducted a survey of marked and radio-collared coyotes over several years to evaluate temporal and spatial factors on capture rates. Time of year for sampling was found to significantly influence captures, relative abundance indices, and density estimates: population numbers fluctuated seasonally with dispersal and births and deaths. Density was highest after whelping, and declined as pups died or dispersed. Captures were highest during the spring before whelping however, most likely due to dispersing transients that could inflate population estimates. The results suggest that it is important to consider the effect time of year can have on detections.

O'Connor, K. M., Nathan, L. R., Liberati, M. R., Tingley, M. W., Vokoun, J. C., & Rittenhouse, T. A. (2017). Camera trap arrays improve detection probability of wildlife: Investigating study design considerations using an empirical dataset. *PloS One*, *12*(4), e0175684.

- Camera trap arrays were set (with arrays consisting of five non-independent cameras within a small plot) to investigate how the use of arrays vs. single cameras, and how the size of camera arrays and how long they are used for, can affect detection probabilities in the eastern United States. When only one camera was used at a site, increasing season length often failed to increase detectability, even after 100 days. It has often been assumed that one camera deployed for a long amount of time was equal to many cameras being deployed for a short amount of time, but the results indicate that this is not the case, and that increasing study length may not help increase metrics like detectability while also threatening to violate closure. The results suggest that studies should focus on other ways of increasing detectability, such as increasing the number of cameras at a site, which was highly effective.

Shannon, G., Lewis, J. S., & Gerber, B. D. (2014). Recommended survey designs for occupancy modelling using motion-activated cameras: Insights from empirical wildlife data. *PeerJ, 2*, e532.

➢ To investigate the effect of survey design on the accuracy and precision of occupancy estimates, 40 cameras were placed across a 160 square kilometre grid. 54 different surveys designs were tested by selectively removing cameras from data analysis. Increasing survey length was found to be the least effective way to decrease uncertainty, while also increasing the likelihood of violating closure. The authors note that when attempting to produce multi-species occupancy estimates, a biologically meaningful sampling period may vary between species, and thus it may be better to define a meaningful season in which to survey, and then consider which species can be reasonably detected within that season.

Si, X., Kays, R., & Ding, P. (2014). How long is enough to detect terrestrial animals? estimating the minimum trapping effort on camera traps. *PeerJ, 2*, e374.

➢ A two-year camera trap data set from a small study plot in Eastern China was used to investigate minimum trapping effort and the effect of adding more cameras to a study. Analysis of the effect of adding new cameras suggests that rotating cameras to new sites, rather than leaving them at their original location, is a much more efficient way of increasing captures. The optimal sampling period for a single site was found to be roughly 40 days.

Steenweg, R., Hebblewhite, M., Whittington, J., Lukacs, P., & McKelvey, K. (2018). Sampling scales define occupancy and underlying occupancy–abundance relationships in animals. *Ecology*, *99*(1), 172-183.

➢ Includes a theoretical overview of occupancy as well as a simulation of point-location data within a SECR framework and then a test of the conclusions with camera trapping

data to investigate further. Sampling for occupancy estimates have no true requirements, but depending on the length of one's survey, the occupancy estimates may differ. Estimates from simulations were found to increase even with constant abundance as survey length increased. Occupancy-abundance relationships were also found to become more curvilinear as survey length increased. The authors suggest that survey length should potentially be such that animals be able to move throughout their home range, but not much longer. This requires knowledge of animal home ranges and movement, but could help avoid the problems that come with surveying for too long.

Weingarth, K., Zeppenfeld, T., Heibl, C., Heurich, M., Bufka, L., Daniszová, K., & Müller, J. (2015). Hide and seek: Extended camera-trap session lengths and autumn provide best parameters for estimating lynx densities in mountainous areas. *Biodiversity and Conservation*, *24*(12), 2935-2952.

- An extensive field study with camera traps set for Eurasian lynx in Central Europe was performed to determine the optimal survey length when considering population closure and the necessary number of recaptures, the optimal time window within the year for stability of density estimates, and the number of trap sites and spacing needed for acceptable estimates. The models suggested autumn was the best time to survey, and that a minimum of 80 days was needed to get enough captures for acceptable estimates, while it was noted that much longer than that would violate closure. These results are most pertinent to medium-sized, low-density carnivores, but the results are encouraging as if low-density predators such as lynx can produce enough captures within a reasonable amount of time to avoid closure, regardless of whether closure is very important or not as some within the literature argue, then studies should be able to be performed in an amount of time that allows them to avoid the question entirely.

Wearn, O., & Glover-Kapfer, P. (2017). Camera-trapping for conservation: A guide to best-practices. *WWF-UK: Woking, UK.*

- A best practices review document, the paper contains recommendations for length of study when attempting to estimate all state variables, as recommendations differ based on objective. However, the document frames the recommendations as overall camera trapping nights, as they are thought of as the product of the necessary number of cameras and the necessary number of days each camera must be active. Refer to Section 1.5, How Many Camera Days?.

2. Data processing

2.1 Metadata standards

Summary: Proper data management is important for efficiency as well as getting the most out of the data produced by a camera trap study. Scotson et al. (2017) produced a review of data management, suggesting nine themes to ensure proper production of metadata and to ensure proper data management. These themes can be used to ensure that no data resolution is lost. More specifically, the suggested metadata standard is the Camera Trap Metadata Standard outlined by Forrester et al. (2016). Not only is it suggested by Wearn & Glover-Kapfer's 2017 best practices document on camera trap management, the most thorough document found in this literature review, but it is also in use by many of the world's largest camera trapping organizations such as The Wildlife Conservation Society, eMammal, the TEAM Network, and others (Forrester et al., 2016). Refer to the paper for a full outline of the metadata standard.

Forrester, T., O'Brien, T., Fegraus, E., Jansen, P. A., Palmer, J., Kays, R., McShea, W. (2016). An open standard for camera trap data. *Biodiversity Data Journal*, (4).

- The paper outlines the Camera Trap Metadata Standard (CTMS), a metadata standard currently in use by some of the largest names in large-scale camera trapping, including the TEAM Network, eMammal, the Wildlife Conservation Society, etc. At its most basic, the CTMS categorizes camera trap data as a four level hierarchy (project, deployment, image sequence, and image), with each level in the hierarchy associated with fields for which metadata must be recorded. The CTMS allows for the importation and storage of data from any organization and any researcher to keep everything as standardized as possible. Refer to the paper for the entire description of the CTMS.

Scotson, L., Johnston, L. R., Iannarilli, F., Wearn, O. R., Mohd-Azlan, J., Wong, W. M., Willard, C. E. (2017). Best practices and software for the management and sharing of camera trap data for small and large scales studies. *Remote Sensing in Ecology and Conservation, 3*(3), 158-172.

- A review of data management and software for collating and sharing data from camera trap studies. From a review of a case study as well as literature review, nine recommendations for the management of camera trap data and its associated metadata were produced: adopt a standardized, non-proprietary and transferable data storage format to store all camera trap data, accompany all spreadsheets with structured metadata, record data at the highest possible resolution, use a clearly documented and consistent geographic coordinate system, maintain a consistent date-time format, record covariate data that might be used to assess detection probability, plan for eventual identification of all bycatch data on non-target species and non-animals, and manage data as one authoritative set, which can be acted on by multiple users consistently and simultaneously.

2.2 Software

Summary: Data management and processing is a critical step in a camera trapping study, and the software that is used is very important for proper data management and processing. There are other methods for the production of metadata and organization of photos, but the use of programmes specifically designed for camera trap photos and associated data are now recognized as the best method to manage those steps of a camera trapping study (Wearn et al., 2017). There are quite a few programmes now that are available for practitioners to use, but many of them have most of the same main functionalities (Scotson et al., 2017). There are relatively few unique features that distinguish different programmes. What features are needed for a specific study will vary depending on what type of survey is to be done, and so choice of software will depend on what the practitioner thinks is most important. One best practices document and two review papers were found to contain reviews of available software, compare them, and contain comparison charts to evaluate the different features of each against the others (Scotson et al., 2017; Wearn & Glover-Kapfer, 2017; Young et al., 2018). Many of the programmes are presented in peer-reviewed journal articles as well for more in-depth descriptions, and these can be found below.

Bubnicki, J. W., Churski, M., & Kuijper, D. P. (2016). Trapper: An open source web-based application to manage camera trapping projects. *Methods in Ecology and Evolution, 7*(10), 1209-1216.

- A paper that outlines TRAPPER, an open-source web-based application that helps to manage, classify, integrate, share, and re-use camera trap data. The authors highlight the main features as being fully open-source, the ability to work with videos as well as images, spatial filtering and mapping, the ability to work with data for any type of study, that it can be multi-user to support collaboration, and that it supports data re-use and

discovery. Refer to the paper for a more in-depth explanation of how it differs from other software.

Fegraus, E. H., Lin, K., Ahumada, J. A., Baru, C., Chandra, S., & Youn, C. (2011). Data acquisition and management software for camera trap data: A case study from the TEAM network. *Ecological Informatics, 6*(6), 345-353.

- A paper that outlines a software system called DeskTEAM, used by the Tropical Ecology Assessment and Monitoring (TEAM) Network. The authors highlight the ability to run the software on a computer without an internet connection, the ability to run on multiple operating systems, an intuitive interface able to work at multiple scales to manage thousands of images, the ability to extract EXIF and custom metadata information from additional information to further standardization, the ability to use embedded taxonomic lists to allow user to tag images, and the ability to export data packages as main features. Refer to the paper for a more in-depth explanation of how it differs from other software.

Ivan, J. S., & Newkirk, E. S. (2016). CPW photo warehouse: A custom database to facilitate archiving, identifying, summarizing and managing photo data collected from camera traps. *Methods in Ecology and Evolution*, *7*(4), 499-504.

- The paper outlines the software C_{PW} Photo Warehouse, which allows for the production of metadata, the importing of photos, and the storage of photos and the associated metadata with a relation database (based in Microsoft Access). Allows for the creation of files needed for occupancy, abundance, density and activity patterns using programmes like MARK, PRESENCE, DENSITY and several R packages. Refer to the paper for a more in-depth explanation of how it differs from other software.

Krishnappa, Y. S., & Turner, W. C. (2014). Software for minimalistic data management in large camera trap studies. *Ecological Informatics, 24*, 11-16.

- The paper outlines the software Aardwolf that can be used to automatically extract metadata from camera trap images, produce and manage more personal metadata, and that is minimalistic, scalable, and extendable. Refer to the paper for a more in-depth explanation of how it differs from other software.

Niedballa, J., Sollmann, R., Courtiol, A., & Wilting, A. (2016). camtrapR: An R package for efficient camera trap data management. *Methods in Ecology and Evolution*, *7*(12), 1457-1462.

- The paper outlines the R package camtrapR, which can be used to manage and process camera trap data, including image organization, species and individual identification, data extraction from images, tabulation and visualization of results and to export data. Other features the authors highlight are the ability to minimize data mistakes with automation and the ability to reduce the need for human input. Refer to the paper for a more in-depth explanation of how it differs from other software.

Scotson, L., Johnston, L. R., Iannarilli, F., Wearn, O. R., Mohd-Azlan, J., Wong, W. M., Willard, C. E. (2017). Best practices and software for the management and sharing of camera trap data for small and large scales studies. *Remote Sensing in Ecology and Conservation, 3*(3), 158-172.

- A review of data management and software for collating and sharing data from camera trap studies. A selection of eight commonly-used programmes were evaluated by their features to produce a comparison chart for practitioners. The authors note that most of the main functionalities of all of the software completely overlap, with a handful of unique

features that practitioners can use to select what works best for them. Refer to the paper for the comparison chart and a more in-depth investigation of the programmes.

Wearn, O., & Glover-Kapfer, P. (2017). Camera-trapping for conservation: A guide to best-practices. *WWF-UK: Woking, UK.*

- A best practices review document, Camera-trapping for Conservation: A Guide to Best-Practices includes an entire chapter dedicated to managing and processing camera trap data. A selection of the most commonly-used programmes were evaluated by feature to produce a comparison chart for practitioners. It is also noted that there are other ways to manage data, such as using general photo-editing software to tag images, or manually enter data into a spreadsheet. However, it is highly recommended to use dedicated camera trap software as it is increasingly becoming the most efficient way to manage data. Refer to the paper for the comparison chart and a more in-depth investigation of the programmes.

Young, S., Rode-Margono, J., & Amin, R. (2018). Software to facilitate and streamline camera trap data management: A review. *Ecology and Evolution*, *8*(19), 9947-9957.

- A recent review (2018) of camera trapping software and an assessment of each's ability to standardize data management and data production and sharing. Includes a review of 12 programmes. Includes a comparison chart for practitioners. eMammal and Agouti were found to be among the most 'advanced' of the programmes. Refer to the paper for the comparison chart and a more in-depth investigation of the programmes.

2.3 Defining event independence

Summary: There was found to be little literature exploring the use of event independence thresholds. Both Burton et al. and Wearn & Glover-Kapfer (2015; 2017) note that 30 or 60 minutes are often used, but times up to 24 hours can also be found within the literature. Identification of individuals as well as non-consecutive photos of the same species can also be found within the literature (Burton et al., 2015). However, very little work has been done investigating what threshold can be supported with scientific reasoning. This literature review found only one study, one that investigated the effect of gregariousness on relative abundance indices (Treves et al., 2010). Gregariousness was found to positively bias RAIs, suggesting that an independence threshold longer than the commonly-used 30 minutes for the same species should be used to counteract it.

Burton, A. C., Neilson, E., Moreira, D., Ladle, A., Steenweg, R., Fisher, J. T., Boutin, S. (2015). Wildlife camera trapping: A review and recommendations for linking surveys to ecological processes. *Journal of Applied Ecology*, *52*(3), 675-685.

- A paper that reviewed 266 camera trapping studies to examine study objectives and methodologies, evaluate the consistency of protocols and sampling designs, and investigate practitioner's linking of analytical assumptions and species ecology. Notes that there were large differences among the papers in their definitions of event independence, but little exploration of reasoning for the choices. 30 or 60 minutes were found to be the most common thresholds, but times of up to 24 hours were used. Other methods such as identification of other individual or non-consecutive photos of the same species were used.

Treves, A., Mwima, P., Plumptre, A. J., & Isoke, S. (2010). Camera-trapping forest–woodland wildlife of western uganda reveals how gregariousness biases estimates of relative abundance and distribution. *Biological Conservation, 143*(2), 521-528.

- A community camera trap survey in western Uganda was used to investigate the effect of gregariousness on relative abundance indices. Gregariousness, when indexed as mean or maximum group size, was found to correlate strongly with RAI. Gregarious species were also found to be captured more on the same day as well as across multiple consecutive days. The authors thus suggest a longer independence interval than 30 minutes for captures of the same species.

Wearn, O., & Glover-Kapfer, P. (2017). Camera-trapping for conservation: A guide to best-practices. *WWF-UK: Woking, UK.*

- A best practices review document, it briefly touches upon the practice of determining event independence for camera trap studies. It notes that for occupancy and capture-recapture analyses, there is no need to consider event independence, as they involve just recording detections or non-detections within a certain amount of time. Event independence is most important for relative abundance indices. Some studies have not set a time limit for detections to be counted as independent, and have counted a detection as independent every time an animal enters the detection zone. This is also what should be done when using random encounter models. However, the document notes that some arbitrary amount of time is often defined as the boundary between dependent and independent events, with a half an hour or one hour being common. It also notes that the defining of event independence will not matter much for the RAI of a quick-moving species such as many carnivores, but will effect RAIs of slow-moving species that move much more randomly.