Cost-efficient effort allocation for camera-trap occupancy surveys of mammals

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Abstract
Camera-traps are increasingly used to survey threatened mammal species and are an important tool for estimating habitat occupancy. To date, cost-efficient occupancy survey effort allocation studies have focused on trade-offs between number of sample units (SUs) and sampling occasions, with simplistic accounts of associated costs which do not reflect camera-trap survey realities. Here we examine camera-trap survey costs as a function of the number of SUs, survey duration and camera-traps per SU, linking costs to precision in occupancy estimation. We evaluate survey effort trade-offs for hypothetical species representing different levels of occupancy (ψ) and detection (p) probability to identify optimal design strategies. We apply our cost function to three threatened species as worked examples. Additionally, we use an extensive camera-trap data set to evaluate independence between multiple camera traps per SU. The optimal number of sampling occasions that result in minimum cost decrease as detection probability increases, irrespective of whether the species is rare (ψ <0.25) or common (ψ >0.5). The most expensive survey scenarios occur for elusive (p <0.25) species with a large home range (>10 km^2), where the survey is conducted on foot. Minimum survey costs for elusive species can be achieved with fewer sampling occasions and multiple cameras per SU. Multiple camera-traps set within a single SU can yield independent species detections. We provide managers and researchers with guidance for conducting cost-efficient camera-trap occupancy surveys. Efficient use of survey budgets will ultimately contribute to the conservation of threatened and data deficient mammals.

Key-words: elusive species, imperfect detection, species management, threatened species, wildlife monitoring

1. Introduction

To conserve threatened species effectively, conservationists must first assess the status of populations. With financial resources generally in short supply, wildlife researchers and managers need to adopt cost-efficient monitoring survey protocols to gather baseline data to inform appropriate conservation interventions (Fryxell, Sinclair & Caughley 2014). Terrestrial mammals can be a particular challenge to survey due to their elusive nature, the fact that they often occur at low densities and, in many cases, are difficult to distinguish individually. As such, population status inferences where individuals are undistinguishable or unmarked rely frequently on presence-absence data and the estimation of species occupancy (i.e. the proportion of sites occupied or used by the species). The value of presence-absence data has increased markedly in recent years as a result of significant developments in occupancy modelling techniques (Vojta 2005) including, for example, being able to account explicitly for the imperfect detection of elusive species (MacKenzie et al. 2006, Guillera-Arroita 2016).

Camera-traps are a widely used tool in ecology and conservation (Rowcliffe & Carbone 2008; O'Connell, Nichols & Karanth 2010; Burton et al. 2015). They are particularly valuable for surveying elusive mammals because they are non-invasive, can work independently in remote areas and perform effectively in comparison to alternative detection methods (Gompper et al. 2006; Long et al. 2007; Balme, Hunter & Slotow 2009). Camera-traps have therefore been deployed in a broad array of circumstances, ranging from monitoring single species populations (Linkie et al. 2013) and constructing mammal inventories in tropical forests (Tobler et al. 2008), through to evaluating the value of modified landscapes for threatened species (Linkie et al.

2007). The number of occupancy studies based on camera-trap data is growing rapidly, with the majority of focal species being unmarked carnivores or ungulates (Burton et al. 2015).

Despite the abundance of camera-trap occupancy studies being conducted and published globally, there is a paucity of research examining how to allocate survey effort to optimize statistical estimation precision taking into account operational costs. In the context of occupancy modelling, survey effort guidelines have been developed to address the trade-off between the number of sample units (hereafter SUs) and the effort applied within each unit (e.g. number of repeat visits per SU) (MacKenzie & Royle 2005; Field, Tyre & Possingham 2005; Bailey et al. 2007; Guillera-Arroita, Ridout & Morgan 2010; Guillera-Arroita & Lahoz-Monfort 2012). All these studies consider simplistic cost functions, where total survey cost is proportional to the total number of survey visits (i.e. number of SUs x survey visits/SU). The underlying assumed scenario is that a field team member revisits the SUs in each sampling occasion. MacKenzie & Royle (2005) go further and account for extra initial set-up costs at each SU, for cases where the first sampling occasion at a SU may be more expensive than subsequent visits. This previous work, whilst useful, does not accurately represent camera-trap surveys where the length of a survey can be extended (i.e. more "sampling occasions" conducted) without directly adding costs. This is because, once installed, camera-traps can work independently for periods of time between installation, maintenance checks and/or retrieval without a specific associated cost.

Another important consideration is that camera-trap survey effort per SU can be increased by both extending survey length and the number of devices deployed per SU. Species with low detection probability require long surveys to obtain precise estimates (Shannon, Lewis & Gerber 2014). This is often the case for species with large home ranges, as they might be difficult to detect due to non-random movement across a large area. By installing independent camera-traps, one can achieve the same level of detection probability with fewer sampling occasions (Long 2008). However, it is unclear where the optimal balance lies between survey length and number of camera-traps per SU once realistic survey costs are accounted for Increasing the number of camera-traps per SU may also be required if the survey length is somehow constrained (e.g. 100 days maximum survey of all SUs).

Here we provide effort allocation guidelines for cost-efficient camera-trap occupancy studies of terrestrial mammals. We develop a detailed cost function for camera-trap surveys, which we parameterise with operational installation efficiency values (e.g. minutes to install a camera-trap) provided by practitioners (e.g. wildlife managers, researchers). This is then used to consider trade-offs in survey effort allocation in terms of optimal survey length and number of camera-traps within a SU needed to achieve occupancy precision targets at minimum costs. We assess a range of occupancy and detection probability scenarios for species with different home range sizes, as well as considering two types of transport between SUs: vehicular and walking. We also discuss survey design alternatives, using three threatened mammals as worked examples, illustrating how our cost function can be employed to identify cost-efficient strategies. For one of the case study species, for which an extensive survey dataset exists, we additionally investigate the deployment of multiple camera-traps per SU. Camera-trap independence is evaluated in terms of detection history similarity and how this varies with: (i) camera placement in contiguous habitat; and, (ii) distance between camera-traps. Our aim is to provide researchers with a transparent and robust tool, which can be adapted to meet project-specific conditions, to inform the efficient use of scarce financial resources when conducting camera-trap occupancy surveys.

2. Methods

2.1 Sample unit definition and survey length

SU size directly influences the interpretation of occupancy as a state variable. SU size also affects the amount of time spent in the field, by increasing field team member movement time both within and between SUs. When it comes to monitoring populations of mammals over large geographic areas, a common recommendation is that the size of the home range should determine the area of, and distance between, independent SUs (MacKenzie et al. 2006). Following this approach, we define the minimum distance between SUs (D_s) as the diameter of the circular area representing the typical home range size of the species R:

$D_s = \sqrt{\frac{4R}{\pi}}(1 + \alpha)$ Eqn. 1,

where α allows including a user-defined buffer as a proportion of home range size that can be used as a conservative approach to account for home range size uncertainty and or extra space to facilitate variable camera placement within the SU (e.g. not in exact centre). For multiple species surveys, just as for single species studies, the size of R must be decided based on the research objectives and what is meaningful for the interpretation of parameters at the community scale (e.g. Burton et. al. 2012).

The duration or length of a particular survey (L) has implications with respect to model assumptions, affecting the interpretation of the estimated occupancy parameter (Guillera-Arroita 2016). The total survey length can be defined as the number of days over which all SUs are surveyed. A maximum length, L_{max}, should be set a priori and in accordance with survey objectives (e.g. whether the aim is to capture a "snapshot" of the system, or identifying the areas used by the species over longer time periods). In practice, to fit occupancy models, the continuous data collected by the camera-traps can be divided into discrete replicate segments, and treated as separate sampling occasions (but see Guillera-Arroita et al. 2011).

2.2 Calculation of survey costs

The total cost of a camera-trap survey is a function of the number of SUs (S), the duration of the survey (and hence the number of sampling occasions K), and the number of camera-traps per SU (n). We can write the cost function in a general form as:

$C_T(S, K, n) = C_F + S \cdot C_{SU}(K, n) + C_V(K, n, S)$ Eqn. 2.

We use C_F to represent fixed costs, which are, those not associated with in-situ operations and particular to each project (e.g. maintenance of a field station or field vehicle, salaries of permanent staff and international flights). Hereafter we do not consider fixed costs because they do not affect optimal design strategy determination as they are independent of the choice of K and n. C_{SU} is the cost of surveying one SU, which is dependent on K and n. We assume that all SUs are surveyed the same amount of time. Finally C_V encompasses other costs associated with the survey that are affected by the final design (see section 2.2.5).

We consider that C_{SU} consists of four types of costs:

$C_{SU}(K, n) = C_1(K, n) + C_2(K, n) + C_3(n) + C_4(K, n)$ Eqn. 3, where $C_1(K,n)$ is camera-trap operational cost within the SU associated with salaries and fuel consumption between sample units during instalment, maintenance, retrieval; $C_2(K,n)$ relates to field logistics during the survey (e.g. travel to survey area and food); $C_3(n)$ comprises camera-trap equipment cost and, $C_4(K,n)$ is post-survey image processing cost. We provide detail about the construction of each of these four elements.

2.2.1 Operational costs per sample unit

Operational cost C_1 includes personnel salaries and fuel consumption associated with installing, retrieving and conducting maintenance service checks for the camera-traps in a single SU. We assume that installation involves the preparation of a single camera-trap (i.e. loading batteries, memory card and checking overall function) and its positioning for the duration of the survey. Retrieval consists of data collection (e.g. downloading the memory card), note-taking and camera-trap removal after the survey is complete. Maintenance involves checking/changing batteries, lures, baits and memory cards during the survey.

To calculate C_1, we compute the time spent at a particular SU during installation H_i, retrieval H_r or maintenance checks H_c:

$$H_x = \left\{ t_x + \frac{d(n-1)}{V_w} + \frac{2D_s}{V_y} \right\} \text{ Eqn. 4,}$$

where: t_x (t_i, t_r, t_c) is the time (hours) spent handling each of the n cameras in the SU; d is the travel distance between a pair of cameras within the SU (km); V_w is walking speed through habitat (km/h) to camera-traps within an SU; D_s is the distance to the next sampling unit (as per eqn. 1); and, V_y is the travel speed between SUs (km/h), which can either be by vehicle ($V_y = V_v$) or walking ($V_y = V_w$). The last term in Eqn. 4 multiplies the diameter of the SU by two. This assumes that the camera-traps are set up sequentially and then the same distance has to be travelled either by vehicle or foot, on the return journey back to the field vehicle, after the last SU has been installed. Once these times have been computed, the total operational time per SU in hours is:

$$H_{SU} = H_i + H_r + \left\lfloor \frac{L}{z} - 1 \right\rfloor H_c \quad \text{Eqn. 5,}$$

The camera-traps may need to be checked more than once during the survey, hence the factor multiplying H_c, where z is the time interval in days between maintenance checks (we use $\lfloor . \rfloor$ to denote that the term $\frac{L}{z}$ is rounded down to the nearest whole number, and minus the last sampling occasion as that cost is included in retrieval). We assume that no maintenance is conducted when the remaining time between the last check and retrieval is less than z. We can translate total time per sample unit (Eqn. 5) into working days as follows:

$$H_{SU}^{[d]} = \frac{H_{SU}}{(W-B)} \frac{1}{E} \quad \text{Eqn. 6,}$$

which accounts for net available work time during a particular day. W is the number of hours in a working day, B is the number of hours per day spent travelling and taking breaks, and E is the estimated efficiency given normal field setbacks (a factor from 0 to 1). We calculate B as $1 + D_t/V_m$, where D_t is the daily return distance travelled between the field accommodation and survey area and V_m is the travel speed on a motorway or main road plus a break for an hour for lunch and rest.

The total operational cost per sample unit is:

$$C_1(K,n) = H_{SU}^{[d]} W m \quad \text{Eqn. 7,}$$

where m is the combined salary per hour of the field team. To reflect real-world security and work efficiency considerations, we assume that a team is composed of at least two people: one qualified field officer (i.e. researcher, park ranger) who can work independently setting up camera-traps, and a non-qualified field assistant (e.g. guide, tracker) who cannot set up camera-traps independently. In addition, where travel between SUs is by vehicle ($V_y = V_v$) a term must be added to Eqn. 7 to account for fuel costs $\frac{2D_S F_l}{F_e}\left(2 + \left\lfloor \frac{L}{z} - 1 \right\rfloor\right)$, where F_l is fuel cost per litre, F_e is fuel efficiency (km/l), and the factor in brackets is the number of site visits (i.e. installation and retrieval (hence 2) and number of maintenance checks).

2.2.2 Travel and food costs per sample unit

Field logistics cost C_2 includes costs associated with travel between fieldwork accommodation and the study area, as well as daily consumables (e.g. meals):

$C_2(K,n) = H_{SU}^{[d]}\left\{G + \frac{D_t F_l}{F_e}\right\}$ Eqn. 8,

where G is the cost of food and daily consumables and $\frac{D_t F_l}{F_e}$ is the fuel cost to the survey area (D_t is return distance).

2.2.3 Camera-trap equipment cost

Camera-trap equipment cost C_3 accounts for the expenditure related to purchasing camera-traps, batteries and memory cards:

$C_3(n) = nC_a$ Eqn. 9,

where C_a is the cost of a single camera-trap unit, with its memory card plus batteries for the entire survey.

2.2.4 Post-survey image processing cost

Post-survey image processing cost C_4 is calculated as:

$C_4(K,n) = \frac{LnI_d I_c}{I_h}$ Eqn. 10,

where I_d is the average number of images taken by a camera-trap per day, I_c is the cost per hour of a trained researcher to process images and I_h is number of images processed per hour (including the identification of species and data entry into a database).

2.2.5 Considerations about vehicle hire requirements

Depending on the number of SUs, it might not be feasible to implement the survey (i.e. installation, maintenance checks and retrieval) with just one field vehicle (an assumed fixed cost) while meeting the constraint about maximum survey length (L_{max}). Here we calculate whether extra vehicles would be required to meet this constraint. We assume one vehicle can only accommodate the transportation of two field teams (four individuals). The employment of extra teams does not affect C_1, C_2, C_3, C_4 because these are calculated on a per SU basis. However, it does impact the number of field vehicles required (in addition to the one considered already available for the project), which we assume are hired. We incorporate this cost in Eqn. 2 and we denote it $C_V(K,n,S)$, acknowledging it as a cost affected by the design of the survey.

We compute the number of teams (n_t) required to conduct the survey comfortably within L_{max} as:

$$n_t = \left\lceil \frac{S\,H_{SU}^{[d]}}{L_{max} E_t} \right\rceil, \text{ Eqn. 11}$$

where $SH_{SU}^{[d]}$ is the total time consumed in conducting the surveys, and L_{max} is the maximum duration allowed for the whole survey. It is unrealistic to expect that all tasks can be scheduled such that a perfect use of the time is achieved. Therefore, rather than calculating the number of teams dividing by L_{max}, we impose a tougher constraint by applying a factor Et, which is a proportion defined a priori (<1). By planning for tasks to take less than $L_{max}E_t$, we assume that real implementation will meet the actual constraint of L_{max}.

The term $C_V(K, n, S)$ can be expressed as:

$$C_V(K, n, S) = \left\lceil \frac{n_t - 2}{2} \right\rceil L_{max}\, E_t\, J \quad \text{Eqn. 12,}$$

where J is the cost of vehicle hire per day. Here and in Eqn. 11 the brackets indicate that the quantity is rounded up. If nt is less than two (one existing vehicle for two teams), we set Cv=0 (see Appendix A).

2.3 Linking survey costs to estimator precision

To evaluate survey design trade-offs, we need to link survey costs to estimator quality. This way we can identify the most cost-efficient survey effort allocation to achieve a given level of precision (or, alternatively, identify the best way to allocate a given amount of effort to maximize estimator precision). MacKenzie & Royle (2005) provide the following approximation for the variance of the occupancy estimator, ψ:

$$var(\psi) = \frac{\psi}{S}\left\{1 - \psi + \frac{1 - p^*}{p^* - Kp(1-p)^{K-1}}\right\} \text{ Eqn. 13,}$$

where p is the probability of detection in a sampling occasion at a SU where the species is present, and $p^* = 1 - (1-p)^K$ is the cumulative probability of detection after K sampling occasions. For our camera-trap survey scenario, the probability p refers to the combined detectability of the n camera-traps per SU. Assuming independence among the cameras, we have:

$$p = 1 - (1 - p_1)^n \text{ Eqn. 14,}$$

where p_1 is the probability of detection with a single camera-trap.

The variance in Eqn. 13 reflects the precision that we can expect in our estimation of occupancy, and is a function of the number of S, number of survey occasions K and number of camera-traps per site n. Now, considering a target estimation precision that we want to achieve (i.e. a target var(ψ)), we can solve Eqn. 13 and express S as a function of K and n:

$$S = \frac{\psi}{var(\psi)}\left\{1 - \psi + \frac{1 - p^*}{p^* - Kp(1-p)^{K-1}}\right\} \text{ Eqn. 15.}$$

We can now substitute S by this expression in the equation for total survey cost (Eqn. 2). This way, we express C_T as a function of just K and n (ψ, p and target variance are given values). By giving values to K and n in the resulting equation, we can assess which combination of K and n leads to lowest total survey costs.

2.4 Evaluation of survey design trade-offs

We apply the methods above (Eqn. 2, 13 and 15) to assess survey effort trade-offs (Fig. 1) for a range of camera-trap surveys scenarios for hypothetical and real species. For illustrative purposes, we select the occupancy estimator quality target of var(ψ) = 0.0056, which corresponds to a standard error of 0.075 in occupancy estimates. We parameterise our cost function based on information acquired from experienced camera-trap surveyors (e.g. researchers, wildlife managers, park rangers, postgraduate students) via an online quantitative questionnaire (further details in Appendix B). We use the means (or medians when outliers were prevalent) of the values recorded for each parameter (Table 1). Appendix A provides R code implementing the cost function. The parameter values in the present study are used by default, but users can adapt them as required to explore specific case studies.

2.4.1 Survey design trade-off evaluation: hypothetical species

We first run our trade-off evaluation for a set of hypothetical species. We consider three levels of home range size values, R = 3, 10 and 30 km^2, to represent small (2-6 kg), medium (10-15 kg) and large (>25kg) species respectively (Gittleman & Harvey 1982; Swihart, Slade & Bergstrom 1988). Within each of those home range size levels, we evaluate all combinations of occupancy ψ and detection p probability based on the values 0.10, 0.25, 0.5, 0.75 and 0.90. Note that detection probability values refer to detection via one camera for one sample occasion (Eqn. 14). In total, 150 survey scenarios were compared (i.e. ψ, p and R). For convenience, we refer to our simulated species as 'rare' (ψ <0.25) or 'common' (ψ > 0.50). Similarly, for detection, we consider species 'elusive' if p <0.25 and 'conspicuous' if p >0.5.

For each scenario, we assess survey costs by increasing number of sampling occasions K and independent camera-traps n per SU. Based on our questionnaire results (Table 1), we set the number of days considered a sampling occasion at five. We limited our evaluation of K to a maximum of 20, keeping thus total survey length below 100 days (L_{max} =100). We considered up to four camera-traps per SU. To ensure costs represent a design where all SUs are surveyed during L_{max} we use Eqn. 12 and set the proportion Et at 0.7, meaning that all field operations need to occur within 70% of L_{max} and extra teams (car hire) will be required for some combinations in order comply with this restriction (Eqn. 13 and 14). We consider travel between SUs both via vehicle V_v and walking V_w to examine the impact of transport type. Any survey that uses a mixture of these transport types would result in intermediate values as walking and vehicle travel represent the two extremes of a continuum.

We identify which pair of K and n results in minimum cost and, for all other combinations, calculated how much greater the cost is compared to the minimum. For illustrative purposes, we classify these quantities into five categories: i) 1-1.5; ii) 1.5-2; iii) 2-3; iv) 3-5; and, v) over 5 times greater than minimum cost (Fig. 2 and 3). We exclude combinations of n and K where the required number of SUs to survey exceeds 400 as this is unrealistic. To evaluate the effect of p on cost per SU under different ψ scenarios, we plot the cost per SU of the identified minimum costs. All models, analyses and graphics are conducted with R version 3.2.0 R Core Team (2015).

2.4.2 Worked examples for three case study territorial mammals

To provide working examples for territorial mammals, we apply the methods to evaluate survey design costs for three threatened carnivores that have been the focus of camera-trap occupancy surveys: guiña (Leopardus guigna) (home range = ~3 km^2) (E. Schüttler unpublished data), marbled cat (Pardofelis marmorata) (home range = 11.9 km^2) (Grassman et al. 2005), and sun bear (Helarctos malayanus) (home range >15 km^2) (Te Wong, Servheen & Ambu 2004). All three species are associated with forest habitat, are threatened or data deficient, and have published occupancy and detection probability estimates (Linkie et al. 2007; Johnson, Vongkhamheng & Saithongdam 2009; Gálvez et al. 2013). In our evaluation, we use values for occupancy, detection probability and the number of days considered a sample occasion as reported in the cited studies. All other parameters of the cost function are kept (Table 1).

2.5 Camera trap independence: the guiña case study

To provide an empirical example of an evaluation of independence between multiple camera-trap capture histories within a SU (an assumption in Eqn. 14) we interrogate the guiña case study in more detail, using data from a camera-trap survey conducted in the temperate forest eco-region of southern Chile (39º15´S, 71º48´W) (N. Gálvez unpublished data). A total of 145 SUs (4 km^2) across agricultural land were randomly chosen from 230 potential SUs, each equivalent to the mean observed guiña home range size (Minimum Convex Polygon 95% mean = 270 ±137 ha; E. Schüttler unpublished data). We conducted a total of four survey seasons (summer 2012, summer 2013, spring 2013, summer 2014), with two camera-traps installed per SU (mean distance apart =230 m ±182 SD). Each SU was surveyed for 10-12 blocks of two days to ensure independence between sampling occasions, based on the known ranging behaviour of the species (E. Schüttler unpublished data).

To assess independence, we estimate a Jaccard similarity index, for each pair of camera-traps in an SU. Detection by both cameras (i.e. “11”), or by just one of them (i.e. “01” or “10”), was compared for each sampling occasion. We apply the Jaccard similarity coefficient, calculated as the number of histories of each type, by the expression “11”/ “11+“01”+“10”. As we are interested in assessing similarity in detection within a SU, non-detections pairs (i.e. “00”) were removed for analysis. As a sampling occasion was set at a two day period, we can assume that camera-trap history dissimilarity (e.g. “01” or “10”) is not due to time related bias (i.e. enough time for individuals to be captured, or not, by a second camera). We plot distance between each pair of camera-traps, and whether or not they were placed within contiguous habitat, against the Jaccard index for each season.

3. Results

The online questionnaire was completed by 53 respondents with experience in conducting camera-trap surveys in 35 countries, spread across all continents. Respondents had, on average, completed six camera-trap surveys (SE = 0.68). Out of the 28 parameter values included in the cost function, 20 were derived from the questionnaires (Table 1).

3.1 Trade-off evaluation: hypothetical species

Our evaluation reveals that, for both types of transport (vehicular and walking) between SUs and across all ψ-p scenarios, the combinations with fewest (K <3) replicate survey occasions and lowest number of camera-traps per SU (n <2), led to unrealistic solutions due to the large number of SUs required (>400) (Fig. 2 and 3). Minimum cost for surveys by foot are on average 1.7 (SD= 0.3) times more expensive than those using a vehicle, when comparing ψ-p scenarios at each home range size. The expenditure per SU of minimum cost combinations decreases as detection probability rises for both types of transport between SUs and ψ scenarios (Fig. 4). The highest cost per SU is at low p particularly for walking scenarios. Across all ψ scenarios, minimum costs per SU fall to ≤1 000 USD per SU when p is >0.5, and variation is negligible as p increases.

In general, and relative to each ψ-p scenario, particularly expensive combinations are more frequent at high levels of K and n, predominantly where p and home range are greater in size. Relatively cheaper cost combinations (i.e. green tiles relative to minimum cost for that scenario) tend to be more frequent for smaller p values across ψ scenarios. Between ψ scenarios, values of minimum cost are highest at mid ψ (i.e. 0.5) and decrease towards 0.1 and 0.9 levels for both types of transport. In all ψ-p scenarios, the values of minimum cost rise with increasing home range size. Indeed, at p levels of 0.1 and 0.25, the largest home range scenario is on average 1.5 (SD =0.3) times more expensive to survey than the smallest. This is in comparison to the largest home range being 1.3 (SD =0.2) more expensive than the smallest home range size scenario for higher p levels (i.e. >0.5). Within each ψ scenario, minimum cost is negatively associated with detection probability, meaning that low p is the most expensive level. Low p, at each ψ scenario, is 2.7 (SD =0.6), 2.9 (SD =0.7) and 3.2 (SD =0.7), times more costly than high p at 3 km^2, 10 km^2 and 30 km^2 home range size respectively. Generally, the K required for minimum cost combinations decreases as p increases across all scenarios.

Minimum cost combinations with multiple camera-traps per SU occur in the most efficient design in 20 of the 150 scenarios tested. All 20 scenarios occur at p<0.25, but across all home range sizes (Fig. 2 and 3). They are primarily associated with walking scenarios (17/20) (Fig. 3). For vehicle travel, multiple camera-traps designs (3/20) occur only at high ψ (0.9) and low p (0.1) at all home range sizes (Fig. 2). Across ψ-p scenarios, cheaper combinations were, in general, reached at lower K than the specific minimum cost combination, but with multiple camera-traps.

3.2 Case study territorial mammals

Scenarios for the case study species illustrate the broad trends obtained for the hypothetical species, such as higher costs being associated with larger home range size and lower p, as well as reduction in required K with an increase in p (Fig. 5). The guiña and marbled cat do not yield minimum cost combinations with multiple camera-traps, with the exception of one walking scenario for marbled cat. The opposite is true for sun bear in all but one vehicle travel scenario. Lower cost combinations are reached with multiple camera-traps at lower K across all three species.

3.3 Camera-trap independence

The guiña study case reveals that a high proportion of capture histories between cameras show no similarity (i.e. equal zero) across seasons (summer2012=0.91; summer2013=0.81; spring2013=0.70; summer2014=0.88; Fig. 6). Histories which demonstrate some level of similarity (i.e. >0.00), the majority within an index of <0.5, are concentrated at distances between devices <300 m. The similarity index tends to decrease when camera-traps are >300 m apart. There is no difference in the similarity index between camera-traps positioned in contiguous and non-contiguous forest habitat (Fig. 6b).

4. Discussion

Initial estimates of parameters (i.e. ψ and p) are key to informing decisions about effort allocation in camera-trap occupancy surveys (MacKenzie & Royle 2005; Guillera-Arroita, Ridout & Morgan 2010). Our work goes further, demonstrating the importance of accounting for camera-trap specific costs and species ranging behaviour to improve cost-efficiency in survey effort allocation. We have identified cost-efficient solutions with trade-offs between number of camera-traps within a SU and the number sampling occasions, particularly for wide ranging elusive species (i.e. home range >10 km^2 and p<0.25) in areas were walking between sampling units is the main mode of transport.

As established by the more simplistic cost functions already published in the literature (MacKenzie & Royle 2005; Guillera-Arroita, Ridout & Morgan 2010), in addition to our study, the optimal number of sampling occasions decreases as detection increases. This implies that precise occupancy estimates can be obtained with just a few sampling occasions for species which are detected easily. However, our results go on to show that the difference in the optimal number of sampling occasions between rare (ψ <0.25) and common (ψ >0.25) species is minimal.

In general, highly elusive species (p <0.1) are the most expensive to survey. When elusive (p <0.25), rare species (ψ <0.25) appear relatively cheaper to survey compared to more common ones (ψ >0.50), given the same target precision for occupancy estimation. Indeed, common species are costly to survey where they have occupancy estimates of 0.5 or 0.75 and are highly elusive (p <0.1). This pattern arises because we chose variance as our metric to represent occupancy estimator quality; the optimal number of sampling occasions drives p* (Eqn. 13) near 1, meaning that the variance approximates that of a binomial proportion, which is highest at mid-levels of occupancy. Consequently, keeping a given precision target across species type (i.e. rare or common) requires a larger sample size at occupancy estimates around 0.5. Different precision target criteria for common versus rare species could be used, depending on specific goals of the survey (Guillera-Arroita & Lahoz-Monfort 2012).

Improvements in species detectability might mitigate the high cost associated with camera-trap occupancy surveys for elusive species. The steep drop in the value of minimum cost combinations for detection probabilities 0.1 to 0.25, across all scenarios, suggest that it would be worthwhile for practitioners to conduct a pilot exercise to test alternative designs with the aim of maximizing focal species detectability prior to conducting a full survey. For instance, this may involve assessing how detection probability is influenced by microhabitat characteristics surround the camera-trap position in the SU, prevailing weather conditions (e.g. O'Connell et al. 2006), camera-trap settings (e.g. Hamel et al. 2013) or increasing capture rates through baits (e.g. du Preez et al. 2014 but see Balme et al. 2014 for further discussion on the use of baits).

For elusive species, it is generally more cost-efficient to conduct occupancy surveys using multiple camera-traps over fewer sampling occasions, irrespective if they are rare or common, particularly when surveys are done on foot. This is driven by the fact that it is more expensive in terms of extra work (i.e. time and salaries) and travel between/within larger SUs to undertake extra sampling occasions. For species with low detectability, a range of relatively cost-efficient design combinations (i.e. green tiles) are available to practitioners, providing flexibility with respect to both the number of sampling occasions and camera-traps. Occasionally, field survey teams may face certain logistical constraints, such as needing to conduct short camera-trap rotations or confine work to periods of favourable weather. This can therefore be overcome by adopting an approach where multiple camera-traps are used per SU but the overall length of the survey is decreased. Another potential constraint which might be faced is the need to reduce number of sampling occasions to ensure occupancy modelling assumptions are more comfortably met for a particular species (Rota et al. 2009).

Our guiña case study shows that achieving independence between multiple camera-traps positioned within a single SU is feasible for species with a small home range. However, we only evaluated the use of two camera-traps, and maintaining independence would become increasingly difficult with more devices. Moreover, care needs to be taken to ensure that they are not located so far apart that the camera-traps in adjacent SUs become too close.

The three case studies evaluated here reveal how our cost function can provide practitioners with efficient survey allocation scenarios for surveying territorial mammals. For each species there are various trade-offs that warrant consideration, depending on the conservation context. For instance, cost effective monitoring of a guiña population would require longer survey lengths because few sampling occasions provides a high number of unrealistic combinations (i.e. $S > 400$ shown as empty combinations). Our knowledge of how marbled cats are distributed across Asia is lacking, and hindering conservation efforts (Johnson, Vongkhamheng & Saithongdam 2009). If field conditions or logistics constraints mean that survey length must be kept short, our cost function show that there are a wide range of cost-efficient options available, centered on fewer sampling occasions and additional camera-traps. Likewise, sun bear surveys, which are required in forested areas outside protected lands (Linkie et al. 2007), could be most cost-efficient with multiple camera-traps per SU. One important point to note is that our framework is developed for constant occupancy models (i.e. with no covariates). In many species-specific cases, practitioners might be interested in appraising the effects of environmental covariates or the impact of management interventions, which may require sampling more SUs for statistical reasons. This would be most expensive for elusive species, due to the costs associated with each SU (Fig. 4). Our cost function can be readily incorporated in the evaluation of survey design trade-offs for more complex models via simulations.

Worldwide, around 15% of mammal species are data deficient and need urgently to have their extinction risk evaluated (Schipper et al. 2008). Our cost function provides practitioners with a valuable tool which can be used to inform the design of cost-efficient camera-trap occupancy surveys, which are required to assess the conservation status of potentially threatened unmarked mammals (Beaudrot et al. 2016). While the evaluation here represents average field survey parameters, as reported by practitioners, it can be readily adapted to account for specific survey conditions and objectives.

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Table 1. Description of constant parameters used to estimate camera-trap survey cost provided by users obtained from an on-line questionnaire and literature reference values.

Type	Terms	Parameter	Number of respondents[a]	Average (SD)	Median	Mode	Min	Max	Value used in the cost function	Comments and units used in the cost function
User experience	Experience (years)	-	53	5 (3)	4	3	1	15	-	For reference use
	Number of completed surveys	-	53	6 (5)	4	3	1	30	-	For reference use
	Year last survey was conducted	-	53	-	-	2014	2005	2015	-	For reference use
Field operation values	Camera-trap installation time (mins)	I	53	40 (36)	30	30	5	180	0.66	Average hours
	Camera-trap retrieval time (mins)	R	53	15 (10)	15	10	2	45	0.25	Average hours
	Maintenance check time (mins)	C	53	13 (11)	10	5	1	60	0.21	Average hours
	Time between maintenance checks (days)	Z	32	17 (12)	15	15	1	50	10	

Overall survey length (days)	L_{max}	45	128 (94)	90	90	30	540	100[c]	
Duration of survey per sampling unit (days)	-	51	58 (56)	45	30	6	300	-	For reference use
Time considered a sampling occasion (days)	O	20	7 (5)	6	5	1	15	5 [b]	Mode
Length work day (hours)	W	53	8 (3)	8	8	1	15	8	Average hours
Proportion of time spent on setbacks	E	52	0.16 (0.12)	0.10	0.10	0.00	0.50	0.84	Efficiency =1-average
Walking speed between sampling units (km/hour)	V_w	-	-	-	-	-	-	3.5	Average km/hour
Vehicle speed between sample units (km/hour)	V_y	37	33 (12)	30	20	15	60	33	Average km/hour
Vehicle speed on main road (km/hour)	V_m	40	64 (27)	60	60	20	120	64	Average km/hour
Fuel efficiency (km/l)	F_e	-	8 (0.93)	8	8	6.3	9.7	8[d]	Average km/l
Distance between field accommodation and survey area (km)	D_t	36	50 (52)	28	20	3	200	56	Median km

Field costs ($USD)	Salary of trained personnel (USD/hour)	m_{tp}	34	10 (8)	8	25	1	30	10	Average USD per hour
	Salary of field assistants (USD/hour)	m_{fa}	29	4 (4)	2	2	0	16	4	Average USD per hour
	Food costs (USD/day)	G	44	16 (19)	10	10	1	109	16[e]	Average USD per person
	Petrol (USD/l)	F_l	36	3 (4)	1	1	0	15	3	Average USD per l
	Cost of renting field vehicle (USD/day)	J	23	86 (80)	50	50	12	350	86	Average USD per day
Camera units	Cost of camera-trap (USD/unit)	C_a	46	350 (214)	257	200	80	931	350[f]	Average USD per unit
Post-survey image processing	Number of images per camera-trap	I_d	43	21 (29)	12	17	0	144	21	Average per day
	Images processed per an hour	I_h	29	396 (532)	100	100	4	2000	396	Average per hour
	Cost of processing images (USD/hour)	I_c	27	12 (14)	6	16	1	60	12[g]	Average USD per hour
Other	Factor to ensure all field activities can be conducted within maximum length of survey	E_t	-	-	-	-	-	-	0.70	Proportion of L_{max}

Extra buffer area around a sample unit (%)	α	-	-	-	-	-	-	0.25	Proportion of sample unit

a) Included for parameter values evaluated via the questionnaire

b) We use the mode of the criteria used to determine the number of days collapsed into one sampling occasion in occupancy studies

c) We use 100 days as maximum length of survey which is within the average and mode.

d) Based on fuel efficiency figures for Jeep, Land Rover, Nissan, Subaru, Toyota and Suzuki petrol sport/pickup/utility vehicles, made between 1995 and 2010. Source: US Department of Energy 2015 (http://www.fueleconomy.gov/)

e) Food cost is doubled in cost function as the field team is assumed to comprise two individuals

f) Includes the camera-trap, SD card and batteries

g) Cost of trained personnel paid to identify species and enter data into a database

Figure 1: Synthesis of steps and parameters used to evaluate cost-efficient and statistically precise camera-trap survey trade-offs for occupancy estimates of terrestrial mammals.

Figure 2: Cost (US dollars) of different camera-trap occupancy survey effort allocations, assuming vehicular transport is employed between sample units (SUs). Each tile represents a combination of number of sampling occasions K and number of camera-traps n per SU. Tile color reflects the cost required to achieve a target statistical precision (S.E. =0.075) in occupancy estimates (ψ) for any given combination of home range size (3, 10, 30 km2), occupancy and detection (p) probabilities. All detection probability values refer to p1 (Eqn. 12) which refers to the detection of one camera for one sample occasion. Costs are shown in relative terms, benchmarked against the cheapest combination indicated in blue: 1-1.5, green; 1.5-2, olive; 2-3, yellow; 3-5, light orange; >5 times greater, orange. Maximum number of K considered is 20 (assuming that each occasion is five days long and a maximum possible survey length is 100 days). Empty combinations indicate solutions that require > 400 sites to be surveyed.

Figure 3: Cost (US dollars) of different camera-trap occupancy survey effort allocations, assuming the distance between sample units is walked. For details regarding the figure arrangement, please refer to the legend for Figure 1.

Figure 4: Range of costs (US dollars) per sample unit (SU) for all minimum cost occupancy (ψ) and detection (p) probability combinations. Both type of transport between SUs (walking and vehicular) are compared.

Figure 5: Camera-trap occupancy survey effort scenarios and combinations for three threatened case study carnivore species: guiña (Leopardus guigna), marbled cat (Pardofelis marmorata) and sun bear (Helarctos malayanus). For details regarding the figure arrangement, please refer to the legend for Figure 1. Both walking and vehicular transport between sample units are evaluated, as well as various combinations of occupancy (ψ) and detection (p) probability derived from the literature for each species. Guiña: 3 km^2 home range (E. Schüttler unpublished data); occupancy and detection parameters with two days considered a sampling occasion (Fleschutz et. al. 2016). Marbled cat: 11.9 km^2 home range (Grassman et al. 2005); occupancy and detection parameters and five days considered a sampling occasion (Johnson et al. 2009). Sun bear: >15 km^2 home range (Te Wong, Servheen & Ambu 2004), occupancy and detection parameters and 15 days considered a sampling occasion (Linkie et al. (2007).

Figure 6: Jaccard similarity index of the camera-trap occupancy survey capture histories for two devices per sample unit (SU), used when surveying guiña (Leopardus guigna) over four seasons. The index is plotted against: (a) distance between camera-traps (m) within each SU, and; b) whether or not the two devices were set up within a contiguous habitat patch in the SU.