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

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20 **Abstract**

21 Camera-traps are increasingly used to survey threatened mammal species and are an important
22 tool for estimating habitat occupancy. To date, cost-efficient occupancy survey effort allocation
23 studies have focused on trade-offs between number of sample units (SUs) and sampling
24 occasions, with simplistic accounts of associated costs which do not reflect camera-trap survey
25 realities. Here we examine camera-trap survey costs as a function of the number of SUs, survey
26 duration and camera-traps per SU, linking costs to precision in occupancy estimation. We
27 evaluate survey effort trade-offs for hypothetical species representing different levels of
28 occupancy (ψ) and detection (p) probability to identify optimal design strategies. We apply our
29 cost function to three threatened species as worked examples. Additionally, we use an extensive
30 camera-trap data set to evaluate independence between multiple camera traps per SU. The
31 optimal number of sampling occasions that result in minimum cost decrease as detection
32 probability increases, irrespective of whether the species is rare ($\psi < 0.25$) or common ($\psi > 0.5$).
33 The most expensive survey scenarios occur for elusive ($p < 0.25$) species with a large home range
34 ($> 10 \text{ km}^2$), where the survey is conducted on foot. Minimum survey costs for elusive species can
35 be achieved with fewer sampling occasions and multiple cameras per SU. Multiple camera-traps
36 set within a single SU can yield independent species detections. We provide managers and
37 researchers with guidance for conducting cost-efficient camera-trap occupancy surveys. Efficient
38 use of survey budgets will ultimately contribute to the conservation of threatened and data
39 deficient mammals.

40

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

43

44 **1. Introduction**

45 To conserve threatened species effectively, conservationists must first assess the status of
46 populations. With financial resources generally in short supply, wildlife researchers and
47 managers need to adopt cost-efficient monitoring survey protocols to gather baseline data to
48 inform appropriate conservation interventions (Fryxell, Sinclair & Caughley 2014). Terrestrial
49 mammals can be a particular challenge to survey due to their elusive nature, the fact that they
50 often occur at low densities and, in many cases, are difficult to distinguish individually. As such,
51 population status inferences where individuals are undistinguishable or unmarked rely frequently
52 on presence-absence data and the estimation of species occupancy (i.e. the proportion of sites
53 occupied or used by the species). The value of presence-absence data has increased markedly in
54 recent years as a result of significant developments in occupancy modelling techniques (Vojta
55 2005) including, for example, being able to account explicitly for the imperfect detection of
56 elusive species (MacKenzie et al. 2006, Guillera-Aroita 2016).

57

58 Camera-traps are a widely used tool in ecology and conservation (Rowcliffe & Carbone 2008;
59 O'Connell, Nichols & Karanth 2010; Burton et al. 2015). They are particularly valuable for
60 surveying elusive mammals because they are non-invasive, can work independently in remote
61 areas and perform effectively in comparison to alternative detection methods (Gompper et al.
62 2006; Long et al. 2007; Balme, Hunter & Slotow 2009). Camera-traps have therefore been
63 deployed in a broad array of circumstances, ranging from monitoring single species populations
64 (Linkie et al. 2013) and constructing mammal inventories in tropical forests (Tobler et al. 2008),
65 through to evaluating the value of modified landscapes for threatened species (Linkie et al.

66 2007). The number of occupancy studies based on camera-trap data is growing rapidly, with the
67 majority of focal species being unmarked carnivores or ungulates (Burton et al. 2015).

68
69 Despite the abundance of camera-trap occupancy studies being conducted and published
70 globally, there is a paucity of research examining how to allocate survey effort to optimize
71 statistical estimation precision taking into account operational costs. In the context of occupancy
72 modelling, survey effort guidelines have been developed to address the trade-off between the
73 number of sample units (hereafter SUs) and the effort applied within each unit (e.g. number of
74 repeat visits per SU) (MacKenzie & Royle 2005; Field, Tyre & Possingham 2005; Bailey et al.
75 2007; Guillera-Arroita, Ridout & Morgan 2010; Guillera-Arroita & Lahoz-Monfort 2012). All
76 these studies consider simplistic cost functions, where total survey cost is proportional to the
77 total number of survey visits (i.e. number of SUs x survey visits/SU). The underlying assumed
78 scenario is that a field team member revisits the SUs in each sampling occasion. MacKenzie &
79 Royle (2005) go further and account for extra initial set-up costs at each SU, for cases where the
80 first sampling occasion at a SU may be more expensive than subsequent visits. This previous
81 work, whilst useful, does not accurately represent camera-trap surveys where the length of a
82 survey can be extended (i.e. more “sampling occasions” conducted) without directly adding
83 costs. This is because, once installed, camera-traps can work independently for periods of time
84 between installation, maintenance checks and/or retrieval without a specific associated cost.

85
86 Another important consideration is that camera-trap survey effort per SU can be increased by
87 both extending survey length and the number of devices deployed per SU. Species with low
88 detection probability require long surveys to obtain precise estimates (Shannon, Lewis & Gerber
89 2014). This is often the case for species with large home ranges, as they might be difficult to
90 detect due to non-random movement across a large area. By installing independent camera-traps,
91 one can achieve the same level of detection probability with fewer sampling occasions (Long
92 2008). However, it is unclear where the optimal balance lies between survey length and number
93 of camera-traps per SU once realistic survey costs are accounted for. Increasing the number of
94 camera-traps per SU may also be required if the survey length is somehow constrained (e.g. 100
95 days maximum survey of all SUs).

96
97 Here we provide effort allocation guidelines for cost-efficient camera-trap occupancy studies of
98 terrestrial mammals. We develop a detailed cost function for camera-trap surveys, which we
99 parameterise with operational installation efficiency values (e.g. minutes to install a camera-trap)
100 provided by practitioners (e.g. wildlife managers, researchers). This is then used to consider
101 trade-offs in survey effort allocation in terms of optimal survey length and number of camera-
102 traps within a SU needed to achieve occupancy precision targets at minimum costs. We assess a
103 range of occupancy and detection probability scenarios for species with different home range
104 sizes, as well as considering two types of transport between SUs: vehicular and walking. We also
105 discuss survey design alternatives, using three threatened mammals as worked examples,
106 illustrating how our cost function can be employed to identify cost-efficient strategies. For one of
107 the case study species, for which an extensive survey dataset exists, we additionally investigate
108 the deployment of multiple camera-traps per SU. Camera-trap independence is evaluated in
109 terms of detection history similarity and how this varies with: (i) camera placement in contiguous
110 habitat; and, (ii) distance between camera-traps. Our aim is to provide researchers with a

111 transparent and robust tool, which can be adapted to meet project-specific conditions, to inform
112 the efficient use of scarce financial resources when conducting camera-trap occupancy surveys.

113

114 **2. Methods**

115 2.1 Sample unit definition and survey length

116 SU size directly influences the interpretation of occupancy as a state variable. SU size also
117 affects the amount of time spent in the field, by increasing field team member movement time
118 both within and between SUs. When it comes to monitoring populations of mammals over large
119 geographic areas, a common recommendation is that the size of the home range should
120 determine the area of, and distance between, independent SUs (MacKenzie et al. 2006).

121 Following this approach, we define the minimum distance between SUs (D_s) as the diameter of
122 the circular area representing the typical home range size of the species R :

$$123 D_s = \sqrt{\frac{4R}{\pi}} (1 + \alpha) \text{ Eqn. 1,}$$

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

130

131 The duration or length of a particular survey (L) has implications with respect to model
132 assumptions, affecting the interpretation of the estimated occupancy parameter (Guillera-Arroita
133 2016). The total survey length can be defined as the number of days over which all SUs are
134 surveyed. A maximum length, L_{max} , should be set a priori and in accordance with survey
135 objectives (e.g. whether the aim is to capture a “snapshot” of the system, or identifying the areas
136 used by the species over longer time periods). In practice, to fit occupancy models, the
137 continuous data collected by the camera-traps can be divided into discrete replicate segments,
138 and treated as separate sampling occasions (but see Guillera-Arroita et al. 2011).

139

140 2.2 Calculation of survey costs

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

$$144 C_T(S, K, n) = C_F + S \cdot C_{SU}(K, n) + C_V(K, n, S) \text{ Eqn. 2.}$$

145

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

153

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

$$155 C_{SU}(K, n) = C_1(K, n) + C_2(K, n) + C_3(n) + C_4(K, n) \text{ Eqn. 3,}$$

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

161

162 2.2.1 Operational costs per sample unit

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

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

$$172 \quad H_x = \left\{ t_x + \frac{d(n-1)}{V_w} + \frac{2D_s}{V_y} \right\} \text{ Eqn. 4,}$$

173 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
 174 travel distance between a pair of cameras within the SU (km); V_w is walking speed through
 175 habitat (km/h) to camera-traps within an SU; D_s is the distance to the next sampling unit (as per
 176 eqn. 1); and, V_y is the travel speed between SUs (km/h), which can either be by vehicle ($V_y = V_v$)
 177 or walking ($V_y = V_w$). The last term in Eqn. 4 multiplies the diameter of the SU by two. This
 178 assumes that the camera-traps are set up sequentially and then the same distance has to be
 179 travelled either by vehicle or foot, on the return journey back to the field vehicle, after the last
 180 SU has been installed. Once these times have been computed, the total operational time per SU
 181 in hours is:

$$182 \quad H_{SU} = H_i + H_r + \left\lfloor \frac{L}{z} - 1 \right\rfloor H_c \text{ Eqn. 5,}$$

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

$$189 \quad H_{SU}^{[d]} = \frac{H_{SU}}{(W-B)} \frac{1}{E} \text{ Eqn. 6,}$$

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

196

197 The total operational cost per sample unit is:

$$198 \quad C_1(K, n) = H_{SU}^{[d]} W m \text{ Eqn. 7,}$$

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

207

208 *2.2.2 Travel and food costs per sample unit*

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

$$211 C_2(K, n) = H_{SU}^{[d]} \left\{ G + \frac{D_t F_l}{F_e} \right\} \text{ Eqn. 8,}$$

212 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
 213 is return distance).

214

215 *2.2.3 Camera-trap equipment cost*

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

$$218 C_3(n) = n C_a \text{ Eqn. 9,}$$

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

221

222 *2.2.4 Post-survey image processing cost*

223 Post-survey image processing cost C_4 is calculated as:

$$224 C_4(K, n) = \frac{\ln I_d I_c}{I_h} \text{ Eqn. 10,}$$

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

228

229 *2.2.5 Considerations about vehicle hire requirements*

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

239

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

242 $n_t = \left\lceil \frac{SH_{SU}^{[d]}}{L_{max}E_t} \right\rceil$, Eqn. 11

243

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

250

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

252 $C_V(K, n, S) = \left\lceil \frac{n_t - 2}{2} \right\rceil L_{max} E_t J$ Eqn. 12,

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

256

257 2.3 Linking survey costs to estimator precision

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

263 $var(\psi) = \frac{\psi}{S} \left\{ 1 - \psi + \frac{1-p^*}{p^* - Kp(1-p)^{K-1}} \right\}$ Eqn. 13,

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

269 $p = 1 - (1 - p_1)^n$ Eqn. 14,

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

271 The variance in Eqn. 13 reflects the precision that we can expect in our estimation of occupancy,
 272 and is a function of the number of S , number of survey occasions K and number of camera-traps
 273 per site n . Now, considering a target estimation precision that we want to achieve (i.e. a target
 274 $var(\psi)$), we can solve Eqn. 13 and express S as a function of K and n :

275 $S = \frac{\psi}{var(\psi)} \left\{ 1 - \psi + \frac{1-p^*}{p^* - Kp(1-p)^{K-1}} \right\}$ Eqn. 15.

276

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

281

282 2.4 Evaluation of survey design trade-offs

283 We apply the methods above (Eqn. 2, 13 and 15) to assess survey effort trade-offs (Fig. 1) for a
 284 range of camera-trap surveys scenarios for hypothetical and real species. For illustrative

285 purposes, we select the occupancy estimator quality target of $\text{var}(\psi) = 0.0056$, which
286 corresponds to a standard error of 0.075 in occupancy estimates. We parameterise our cost
287 function based on information acquired from experienced camera-trap surveyors (e.g.
288 researchers, wildlife managers, park rangers, postgraduate students) via an online quantitative
289 questionnaire (further details in Appendix B). We use the means (or medians when outliers were
290 prevalent) of the values recorded for each parameter (Table 1). Appendix A provides R code
291 implementing the cost function. The parameter values in the present study are used by default,
292 but users can adapt them as required to explore specific case studies.

293

294 *2.4.1 Survey design trade-off evaluation: hypothetical species*

295 We first run our trade-off evaluation for a set of hypothetical species. We consider three levels of
296 home range size values, $R = 3, 10$ and 30 km^2 , to represent small (2-6 kg), medium (10-15 kg)
297 and large ($>25\text{kg}$) species respectively (Gittleman & Harvey 1982; Swihart, Slade & Bergstrom
298 1988). Within each of those home range size levels, we evaluate all combinations of occupancy
299 ψ and detection p probability based on the values 0.10, 0.25, 0.5, 0.75 and 0.90. Note that
300 detection probability values refer to detection via one camera for one sample occasion (Eqn. 14).
301 In total, 150 survey scenarios were compared (i.e. ψ, p and R). For convenience, we refer to our
302 simulated species as ‘rare’ ($\psi < 0.25$) or ‘common’ ($\psi > 0.50$). Similarly, for detection, we
303 consider species ‘elusive’ if $p < 0.25$ and ‘conspicuous’ if $p > 0.5$.

304

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

316

317 We identify which pair of K and n results in minimum cost and, for all other combinations,
318 calculated how much greater the cost is compared to the minimum. For illustrative purposes, we
319 classify these quantities into five categories: i) 1-1.5; ii) 1.5-2; iii) 2-3; iv) 3-5; and, v) over 5
320 times greater than minimum cost (Fig. 2 and 3). We exclude combinations of n and K where the
321 required number of SUs to survey exceeds 400 as this is unrealistic. To evaluate the effect of p
322 on cost per SU under different ψ scenarios, we plot the cost per SU of the identified minimum
323 costs. All models, analyses and graphics are conducted with R version 3.2.0 R Core Team
324 (2015).

325

326 *2.4.2 Worked examples for three case study territorial mammals*

327 To provide working examples for territorial mammals, we apply the methods to evaluate survey
328 design costs for three threatened carnivores that have been the focus of camera-trap occupancy
329 surveys: guiña (*Leopardus guigna*) (home range = $\sim 3 \text{ km}^2$) (E. Schüttler unpublished data),
330 marbled cat (*Pardofelis marmorata*) (home range = 11.9 km^2) (Grassman et al. 2005), and sun

331 bear (*Helarctos malayanus*) (home range >15 km²) (Te Wong, Servheen & Ambu 2004). All
332 three species are associated with forest habitat, are threatened or data deficient, and have
333 published occupancy and detection probability estimates (Linkie et al. 2007; Johnson,
334 Vongkhamheng & Saithongdam 2009; Gálvez et al. 2013). In our evaluation, we use values for
335 occupancy, detection probability and the number of days considered a sample occasion as
336 reported in the cited studies. All other parameters of the cost function are kept (Table 1).

337

338 2.5 Camera trap independence: the guiña case study

339 To provide an empirical example of an evaluation of independence between multiple camera-trap
340 capture histories within a SU (an assumption in Eqn. 14) we interrogate the guiña case study in
341 more detail, using data from a camera-trap survey conducted in the temperate forest eco-region
342 of southern Chile (39°15'S, 71°48'W) (N. Gálvez unpublished data). A total of 145 SUs (4 km²)
343 across agricultural land were randomly chosen from 230 potential SUs, each equivalent to the
344 mean observed guiña home range size (Minimum Convex Polygon 95% mean = 270 ±137 ha; E.
345 Schüttler unpublished data). We conducted a total of four survey seasons (summer 2012, summer
346 2013, spring 2013, summer 2014), with two camera-traps installed per SU (mean distance apart
347 =230 m ±182 SD). Each SU was surveyed for 10-12 blocks of two days to ensure independence
348 between sampling occasions, based on the known ranging behaviour of the species (E. Schüttler
349 unpublished data).

350

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

361

362 3. Results

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

367

368 3.1 Trade-off evaluation: hypothetical species

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

377 minimum costs per SU fall to $\leq 1\ 000$ USD per SU when p is >0.5 , and variation is negligible as
378 p increases.

379
380 In general, and relative to each ψ - p scenario, particularly expensive combinations are more
381 frequent at high levels of K and n , predominantly where p and home range are greater in size.
382 Relatively cheaper cost combinations (i.e. green tiles relative to minimum cost for that scenario)
383 tend to be more frequent for smaller p values across ψ scenarios. Between ψ scenarios, values of
384 minimum cost are highest at mid ψ (i.e. 0.5) and decrease towards 0.1 and 0.9 levels for both
385 types of transport. In all ψ - p scenarios, the values of minimum cost rise with increasing home
386 range size. Indeed, at p levels of 0.1 and 0.25, the largest home range scenario is on average 1.5
387 (SD =0.3) times more expensive to survey than the smallest. This is in comparison to the largest
388 home range being 1.3 (SD =0.2) more expensive than the smallest home range size scenario for
389 higher p levels (i.e. >0.5). Within each ψ scenario, minimum cost is negatively associated with
390 detection probability, meaning that low p is the most expensive level. Low p , at each ψ scenario,
391 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 km², 10
392 km² and 30 km² home range size respectively. Generally, the K required for minimum cost
393 combinations decreases as p increases across all scenarios.

394
395 Minimum cost combinations with multiple camera-traps per SU occur in the most efficient
396 design in 20 of the 150 scenarios tested. All 20 scenarios occur at $p < 0.25$, but across all home
397 range sizes (Fig. 2 and 3). They are primarily associated with walking scenarios (17/20) (Fig. 3).
398 For vehicle travel, multiple camera-traps designs (3/20) occur only at high ψ (0.9) and low p
399 (0.1) at all home range sizes (Fig. 2). Across ψ - p scenarios, cheaper combinations were, in
400 general, reached at lower K than the specific minimum cost combination, but with multiple
401 camera-traps.

402
403 **3.2 Case study territorial mammals**
404 Scenarios for the case study species illustrate the broad trends obtained for the hypothetical
405 species, such as higher costs being associated with larger home range size and lower p , as well as
406 reduction in required K with an increase in p (Fig. 5). The guiña and marbled cat do not yield
407 minimum cost combinations with multiple camera-traps, with the exception of one walking
408 scenario for marbled cat. The opposite is true for sun bear in all but one vehicle travel scenario.
409 Lower cost combinations are reached with multiple camera-traps at lower K across all three
410 species.

411
412 **3.3 Camera-trap independence**
413 The guiña study case reveals that a high proportion of capture histories between cameras show
414 no similarity (i.e. equal zero) across seasons (summer2012=0.91; summer2013=0.81;
415 spring2013=0.70; summer2014=0.88; Fig. 6). Histories which demonstrate some level of
416 similarity (i.e. >0.00), the majority within an index of <0.5 , are concentrated at distances
417 between devices <300 m. The similarity index tends to decrease when camera-traps are >300 m
418 apart. There is no difference in the similarity index between camera-traps positioned in
419 contiguous and non-contiguous forest habitat (Fig. 6b).

420
421 **4. Discussion**

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

430

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

438

439 In general, highly elusive species ($p < 0.1$) are the most expensive to survey. When elusive (p
440 < 0.25), rare species ($\psi < 0.25$) appear relatively cheaper to survey compared to more common
441 ones ($\psi > 0.50$), given the same target precision for occupancy estimation. Indeed, common
442 species are costly to survey where they have occupancy estimates of 0.5 or 0.75 and are highly
443 elusive ($p < 0.1$). This pattern arises because we chose variance as our metric to represent
444 occupancy estimator quality; the optimal number of sampling occasions drives p^* (Eqn. 13) near
445 1, meaning that the variance approximates that of a binomial proportion, which is highest at mid-
446 levels of occupancy. Consequently, keeping a given precision target across species type (i.e. rare
447 or common) requires a larger sample size at occupancy estimates around 0.5. Different precision
448 target criteria for common versus rare species could be used, depending on specific goals of the
449 survey (Guillera-Arroita & Lahoz-Monfort 2012).

450

451 Improvements in species detectability might mitigate the high cost associated with camera-trap
452 occupancy surveys for elusive species. The steep drop in the value of minimum cost
453 combinations for detection probabilities 0.1 to 0.25, across all scenarios, suggest that it would be
454 worthwhile for practitioners to conduct a pilot exercise to test alternative designs with the aim of
455 maximizing focal species detectability prior to conducting a full survey. For instance, this may
456 involve assessing how detection probability is influenced by microhabitat characteristics
457 surround the camera-trap position in the SU, prevailing weather conditions (e.g. O'Connell et al.
458 2006), camera-trap settings (e.g. Hamel et al. 2013) or increasing capture rates through baits (e.g.
459 du Preez et al. 2014 but see Balme et al. 2014 for further discussion on the use of baits).

460

461 For elusive species, it is generally more cost-efficient to conduct occupancy surveys using
462 multiple camera-traps over fewer sampling occasions, irrespective if they are rare or common,
463 particularly when surveys are done on foot. This is driven by the fact that it is more expensive in
464 terms of extra work (i.e. time and salaries) and travel between/within larger SUs to undertake
465 extra sampling occasions. For species with low detectability, a range of relatively cost-efficient
466 design combinations (i.e. green tiles) are available to practitioners, providing flexibility with
467 respect to both the number of sampling occasions and camera-traps. Occasionally, field survey

468 teams may face certain logistical constraints, such as needing to conduct short camera-trap
469 rotations or confine work to periods of favourable weather. This can therefore be overcome by
470 adopting an approach where multiple camera-traps are used per SU but the overall length of the
471 survey is decreased. Another potential constraint which might be faced is the need to reduce
472 number of sampling occasions to ensure occupancy modelling assumptions are more
473 comfortably met for a particular species (Rota et al. 2009).

474
475 Our guiña case study shows that achieving independence between multiple camera-traps
476 positioned within a single SU is feasible for species with a small home range. However, we only
477 evaluated the use of two camera-traps, and maintaining independence would become
478 increasingly difficult with more devices. Moreover, care needs to be taken to ensure that they are
479 not located so far apart that the camera-traps in adjacent SUs become too close.

480
481 The three case studies evaluated here reveal how our cost function can provide practitioners with
482 efficient survey allocation scenarios for surveying territorial mammals. For each species there
483 are various trade-offs that warrant consideration, depending on the conservation context. For
484 instance, cost effective monitoring of a guiña population would require longer survey lengths
485 because few sampling occasions provides a high number of unrealistic combinations (i.e. $S > 400$
486 shown as empty combinations). Our knowledge of how marbled cats are distributed across Asia
487 is lacking, and hindering conservation efforts (Johnson, Vongkhamheng & Saithongdam 2009).
488 If field conditions or logistics constraints mean that survey length must be kept short, our cost
489 function show that there are a wide range of cost-efficient options available, centered on fewer
490 sampling occasions and additional camera-traps. Likewise, sun bear surveys, which are required
491 in forested areas outside protected lands (Linkie et al. 2007), could be most cost-efficient with
492 multiple camera-traps per SU. One important point to note is that our framework is developed for
493 constant occupancy models (i.e. with no covariates). In many species-specific cases, practitioners
494 might be interested in appraising the effects of environmental covariates or the impact of
495 management interventions, which may require sampling more SUs for statistical reasons. This
496 would be most expensive for elusive species, due to the costs associated with each SU (Fig. 4).
497 Our cost function can be readily incorporated in the evaluation of survey design trade-offs for
498 more complex models via simulations.

499
500 Worldwide, around 15% of mammal species are data deficient and need urgently to have their
501 extinction risk evaluated (Schipper et al. 2008). Our cost function provides practitioners with a
502 valuable tool which can be used to inform the design of cost-efficient camera-trap occupancy
503 surveys, which are required to assess the conservation status of potentially threatened unmarked
504 mammals (Beaudrot et al. 2016). While the evaluation here represents average field survey
505 parameters, as reported by practitioners, it can be readily adapted to account for specific survey
506 conditions and objectives.

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518

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617 *of Wildlife Management*, 69, 845-848.

618 **Table 1.** Description of constant parameters used to estimate camera-trap survey cost provided by users obtained from an on-line
 619 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>I</i>	53	40 (36)	30	30	5	180	0.66	Average hours
	Camera-trap retrieval time (mins)	<i>R</i>	53	15 (10)	15	10	2	45	0.25	Average hours
	Maintenance check time (mins)	<i>C</i>	53	13 (11)	10	5	1	60	0.21	Average hours
	Time between maintenance checks (days)	<i>Z</i>	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

620

621

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

624 **Figure 2:** Cost (US dollars) of different camera-trap occupancy survey effort allocations,
625 assuming vehicular transport is employed between sample units (SUs). Each tile represents a
626 combination of number of sampling occasions K and number of camera-traps n per SU. Tile
627 color reflects the cost required to achieve a target statistical precision (S.E. =0.075) in occupancy
628 estimates (ψ) for any given combination of home range size (3, 10, 30 km²), occupancy and
629 detection (p) probabilities. All detection probability values refer to p_1 (Eqn. 12) which refers to
630 the detection of one camera for one sample occasion. Costs are shown in relative terms,
631 benchmarked against the cheapest combination indicated in blue: 1-1.5, green; 1.5-2, olive; 2-3,
632 yellow; 3-5, light orange; >5 times greater, orange. Maximum number of K considered is 20
633 (assuming that each occasion is five days long and a maximum possible survey length is 100
634 days). Empty combinations indicate solutions that require > 400 sites to be surveyed.

635

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

639

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

643

644 **Figure 5:** Camera-trap occupancy survey effort scenarios and combinations for three threatened
645 case study carnivore species: guiña (*Leopardus guigna*), marbled cat (*Pardofelis marmorata*) and
646 sun bear (*Helarctos malayanus*). For details regarding the figure arrangement, please refer to the
647 legend for Figure 1. Both walking and vehicular transport between sample units are evaluated, as
648 well as various combinations of occupancy (ψ) and detection (p) probability derived from the
649 literature for each species. Guiña: 3 km² home range (E. Schüttler unpublished data); occupancy
650 and detection parameters with two days considered a sampling occasion (Fleschutz et al. 2016).
651 Marbled cat: 11.9 km² home range (Grassman et al. 2005); occupancy and detection parameters
652 and five days considered a sampling occasion (Johnson et al. 2009). Sun bear: >15 km² home
653 range (Te Wong, Servheen & Ambu 2004), occupancy and detection parameters and 15 days
654 considered a sampling occasion (Linkie et al. (2007).

655

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

660