Recommended survey designs for occupancy modelling using motion-activated cameras: insights from empirical wildlife data

Motion-activated cameras are a versatile tool that wildlife biologists can use for sampling wild animal populations to estimate species occurrence. Occupancy modelling provides a flexible framework for the analysis of these data; explicitly recognizing that given a species occupies an area the probability of detecting it is often less than one. Despite the number of studies using camera data in an occupancy framework, there is only limited guidance from the scientific literature about survey design trade-offs when using motion-activated cameras. A fuller understanding of these trade-offs will allow researchers to maximise available resources and determine whether the objectives of a monitoring program or research study are achievable. We use an empirical dataset collected from 40 cameras deployed across 160 km^2 of the Western Slope of Colorado, USA to explore how survey effort (number of cameras deployed and the length of sampling period) affects the accuracy and precision (i.e. error) of the occupancy estimate for ten mammal and three virtual species. We do this using a simulation approach where species occupancy and detection parameters were informed by empirical data from motion-activated cameras. A total of 54 survey designs were considered by varying combinations of sites (10-120 cameras) and occasions (20-120 survey days). Our findings demonstrate that increasing total sampling effort generally decreases error associated with the occupancy estimate, but changing the number of sites or sampling duration can have very different results, depending on whether a species is spatially common or rare (occupancy = ψ) and easy or hard to detect when available (detection probability = p). For rare species with a low probability of detection (i.e., raccoon and spotted skunk) the required survey effort includes maximizing the number of sites and the number of survey days, often to a level that may be logistically unrealistic for many studies. For common species with low detection (i.e., bobcat and coyote) the most efficient sampling approach was to increase the number of occasions (survey days). However, for common species that are moderately detectable (i.e., cottontail rabbit and mule deer), occupancy could reliably be estimated with comparatively low numbers of cameras over a short sampling period. We provide general guidelines for reliably estimating occupancy across a range of terrestrial species (rare to common: ψ = 0.175-0.970, and low to moderate detectability: p = 0.003-0.200) using motion-activated cameras. Wildlife researchers/managers with limited knowledge of the relative abundance and likelihood of detection of a particular species can apply these guidelines regardless of location. We emphasize the importance of prior biological knowledge, defined objectives and detailed planning (e.g. simulating different study-design scenarios) for designing effective monitoring programs and research studies.

Recommended survey designs for occupancy modelling using motion-activated cameras: insights from empirical wildlife data

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Abstract

Motion-activated cameras are a versatile tool that wildlife biologists can use for sampling wild animal populations to estimate species occurrence. Occupancy modelling provides a flexible framework for the analysis of these data; explicitly recognizing that given a species occupies an area the probability of detecting it is often less than one. Despite the number of studies using camera data in an occupancy framework, there is only limited guidance from the scientific literature about survey design trade-offs when using motion-activated cameras. A fuller understanding of these trade-offs will allow researchers to maximise available resources and determine whether the objectives of a monitoring program or research study are achievable. We use an empirical dataset collected from 40 cameras deployed across 160 km^2 of the Western Slope of Colorado, USA to explore how survey effort (number of cameras deployed and the length of sampling period) affects the accuracy and precision (i.e. error) of the occupancy estimate for ten mammal and three virtual species. We do this using a simulation approach where species occupancy and detection parameters were informed by empirical data from motion-activated cameras. A total of 54 survey designs were considered by varying combinations of sites (10-120 cameras) and occasions (20-120 survey days). Our findings demonstrate that increasing total sampling effort generally decreases error associated with the occupancy estimate, but changing the number of sites or sampling duration can have very different results, depending on whether a species is spatially common or rare (occupancy = ψ) and easy or hard to detect when available (detection probability = p). For rare species with a low probability of detection (i.e., raccoon and spotted skunk) the required survey effort includes maximizing the number of sites and the number of survey days, often to a level that may be logistically unrealistic for many studies. For common species with low detection (i.e., bobcat and coyote) the most efficient sampling approach was to increase the number of occasions (survey days). However, for common species that are moderately detectable (i.e., cottontail rabbit and mule deer), occupancy could reliably be estimated with comparatively low numbers of cameras over a short sampling period. We provide general guidelines for reliably estimating occupancy across a range of terrestrial species (rare to common: ψ = 0.175-0.970, and low to moderate detectability: p = 0.003-0.200) using motion-activated cameras. Wildlife researchers/managers with limited knowledge of the relative abundance and likelihood of detection of a particular species can apply these guidelines regardless of location. We emphasize the importance of prior biological knowledge, defined objectives and detailed planning (e.g. simulating different study-design scenarios) for designing effective monitoring programs and research studies.

Introduction

Estimating the distribution of a species or suite of species across the landscape provides wildlife biologists with crucial information for monitoring and conserving animal populations (Noon *et al.* 2012). It is also a key criteria for global conservation initiatives such as the International Union for Conservation of Nature red list (http://www.iucnredlist.org/), which has been used to track the change in extinction risk of threatened species over time (Di Marco *et al.* 2014). Motion-activated cameras are one of the fastest growing techniques for surveying a wide range of terrestrial animals, particularly those that are rare, elusive or cryptic (O'Connell *et al.* 2011; Jamie 2012). The advancement of affordable and reliable digital camera technology in combination with infrared triggers and time delays has enabled biologists to deploy multiple cameras simultaneously to collect data in an efficient and minimally invasive manner. These data have allowed biologists to investigate a diversity of ecological and conservation driven questions, relating to species abundance (Gerber *et al.* 2010) and density (O'Brien & Kinnaird 2011), animal behaviour (Maffei *et al.* 2011), survival (Gardner *et al.* 2010), temporal activity (Ridout & Linkie 2009), and landscape-level occurrence (Thorn *et al.* 2009). Cameras are typically more efficient than traditional sampling methods (e.g. direct observation, radio telemetry) as continuous data can simultaneously be collected on multiple species (e.g. large bodied carnivores; O'Brien & Kinnaird 2011). The field deployment can be standardised and readily replicated, enabling researchers to monitor whether there are changes in the occurrence of target indicator species over both time and space (Ahumada *et al.* 2011; Ahumada, Hurtado & Lizcano 2013).

Occupancy modelling, which uses detection/non-detection data to estimate species occurrence, offers a very useful analytical framework for analysing data collected from motion-activated cameras (O'Connell & Bailey 2011). Occupancy models explicitly recognize that given a species occurs in an area, the probability of detecting it on a single survey is often less than one. This potential source of bias is addressed by using repeat sampling across multiple sites, enabling detection probability to be calculated and incorporated in the occupancy estimate (MacKenzie *et al.* 2006). Among the key benefits of occupancy studies is that detection/non detection data can generally be collected with greater ease and cost effectiveness for a greater number of species than the more detailed demographic data that are commonly required for estimates of abundance and density (Jones 2011). As a result, occupancy modelling is increasingly used to evaluate species distribution (Long *et al.* 2010), habitat use (Betts *et al.* 2008) and population dynamics (MacKenzie *et al.* 2010). The results from these studies and monitoring programs have the potential to be used by wildlife managers and conservation practitioners to determine changes in the distribution of key animal populations as well as strengthening future demographic predictions (Jones 2011; Noon *et al*. 2012).

There are clear advantages to using motion-activated cameras in occupancy studies; nevertheless, in common with other survey techniques, the efficacy of these studies and monitoring programs relies on appropriate and detailed survey design. These considerations include deciding upon what time period to sample, the sampling length, and the number of cameras to deploy, which is dependent on the target species and the type of inference that is sought (MacKenzie *et al*. 2006). For community studies, it is important to recognize that an optimal survey for one species may not be so for another; designing a community-level occupancy study will likely incur trade-offs in efficiency and the scope of inference depending on how well the sampling period and duration coincides with a meaningful biological time frame for each species. Research studies and monitoring programs that are initiated without well-defined objectives and rigorous survey design increase the likelihood of returning results that are insufficient to make meaningful inference on the species or system of interest (Yoccoz, Nichols & Boulinier 2001; Kéry & Schmid 2004; Mattfeldt, Bailey & Grant 2009). Moreover, as conservation and research programs are often limited by the availability of funding, it is crucial that surveys are justified in terms of the costs and benefits of acquiring the data (Nichols & Williams 2006; McDonald-Madden *et al*. 2010).

The necessity of replication in occupancy studies generates a trade-off in survey effort between the number of sites to sample and the number of replicates to conduct at each site (MacKenzie *et al*. 2002; 2003; Tyre *et al*. 2003; MacKenzie *et al*. 2006). A further consideration is that occupancy is assumed to be static during the designated sampling period (assumption of closure; MacKenzie *et al*. 2002), and the length of this period may vary depending upon the species and biological timeframe of interest (e.g. the breeding season; Webber, Heath & Fischer 2013). There are a number of studies that provide theoretical background to study design using an occupancy-modelling framework, highlighting the importance of balancing temporal and spatial replication to most efficiently achieve defined objectives (MacKenzie & Royle 2005; Bailey *et al*. 2007; Guillera-Arroita, Ridout & Morgan 2010; Guillera-Arroita & Lahoz-Monfort 2012). However, there are few studies that have used empirical data from a suite of species to evaluate the effects of varying the number of sites and occasions on the accuracy and precision of occupancy estimates. Moreover, the majority of research exploring the effective use of motion-activated cameras has focussed on 1) comparing cameras with other sampling approaches (Rovero & Marshall 2009; Janečka *et al*. 2011), 2) investigating sampling efficiency as a function of biological parameters (e.g. species, sex, habitat, and season; Larrucea *et al*. 2007; Kelly &

Holub 2008), and 3) evaluating alternative approaches to species inventories (Tobler *et al*. 2008; Si, Kays & Ding 2014). However, a recent analyses conducted on a dataset of avian and mammalian scavengers in sub-arctic environments provided the first detailed discussion of guidelines to determine the optimal survey design for estimating occupancy using empirical data collected from time-triggered cameras (Hamel *et al*. 2013).

We now build on previous research using an extensive dataset collected from motion-activated cameras to explore how survey design influences the accuracy and precision (i.e. error) of occupancy estimates across a range of mammal species. Our specific research objective is to evaluate how varying the number of sampling sites (10-120 cameras) in combination with the number of occasions (20-120 survey days) influences the error associated with estimating occupancy for 10 mammal species and three 'virtual' species. These thirteen species characterize a range of comparatively rare-to-common species with low-to-moderate detection probability, which are typically encountered during camera sampling of terrestrial mammals. Using these results, we provide recommendations and general guidelines that can be used by wildlife practitioners to design and implement studies to evaluate mammal occurrence using motion-activated cameras.

Methods

Study Site

The study site was located on the Western Slope (WS) of Colorado, USA on the Uncompahgre Plateau near the towns of Montrose and Ridgway (Figure 1). The area was characterized by mesas, canyons, and ravines, with elevations ranging from 1800 m to 2600 m and annual precipitation of 430 mm arriving primarily from winter snows and summer thunderstorms (NOAA National Climatic Data). The vegetation communities were dominated by pinyon pine (*Pinus edulis*) and juniper (*Juniperus osteosperma*), ponderosa pine (*Pinus ponderosa*), aspen (*Populus tremuloides*), gambel oak (*Quercus gambelii*), and big sagebrush (*Artemesia tridentata*). The WS had extensive areas of undeveloped natural habitat managed by the Bureau of Land Management, US Forest Service, and private landowners. Paved and unimproved roads occurred throughout the WS. The WS has a history of ranching with some private ranches converted into exurban and rural housing developments.

Study Design

We deployed 40 motion-activated cameras across two survey grids totaling 160 km^2, with individual camera sites spaced approximately 2 km apart. The sampling design was specifically focused on surveying mountain lions (*Puma concolor*) and bobcats (*Lynx rufus*) with cameras placed along game trails, hiking trails, and secondary dirt roads. The placement of cameras along likely travel routes of mammals is common in camera studies and often leads to detecting a diverse assemblage of the mammalian community (O'Connell, Nichols & Karanth 2011). We checked cameras approximately every two weeks to replace memory cards and batteries if required. The sampling approach was passive in that we did not use attractants (i.e., sight, sound, scent) to lure animals to the camera location. Motion-activated cameras operated from August 21 to December 13, 2009. As the study involved non-invasive sampling using motion-activated cameras there was no requirement for institutional review of the proposed research. Data collection was funded by a grant from the National Science Foundation (NSF EF-0723676).

Data and statistical analyses

We took a two-step approach in our analyses. First, the empirical data collected from motion-activated cameras were used to estimate daily detection probabilities and occupancy estimates for a range of terrestrial mammal species with closure assumed for the entire sampling period (i.e. no changes in occupancy). Second, this information was used in simulations to evaluate optimal survey design approaches for the different species. Photographic data were analysed for ten mammal species (see Figure 2; the number of photographs are provided in parentheses), raccoons (*Procyon lotor*: 8), spotted skunks (*Spilogale putorius*: 25), mountain lions (83), black bears (*Ursus americanus*: 96), gray foxes (*Urocyon cinereoargenteus*: 144), coyotes (*Canis latrans*: 192), elk (*Cervus canadensis*: 196), bobcats (225), cottontail rabbits (*Sylvilagus nuttallii*: 1267) and mule deer (*Odocoileus hemionus*: 1753). A sampling occasion was defined as a 24h period, which we refer to as a survey day. Species-specific detection histories were generated for each of the 40 cameras across the four-month sampling period (except black bears, where only the first two months of data were used due to animals hibernating in November and December). For a given species, detection histories provide a record of whether the species was detected (1) or not detected (0) on each survey day for each camera location (40 detection histories for each species). These detection histories were then used to estimate a constant occupancy (ψ_i) and constant detection probability (p_i) for each species i from $i = 1, 2, \ldots, 10$ using the single-species, single-season occupancy model (MacKenzie *et al*. 2002). In addition, we created three 'virtual' species that were not characterized by our empirical data, but that researchers might encounter, to provide examples where daily detection probability is relatively high (>0.1), while occupancy levels are low to moderate (≤0.6; Figure 3). We constructed models using the RMark package (Laake and

Rexstad 2013) in the R programming language (R Development Core Team 2013), which interfaces with Program MARK (White and Burnham 1999). The resulting 13 species provide a range of daily detection probabilities and occupancy estimates that are typical for mammals surveyed with motion-activated cameras. The species are classified into seven distinct groups ranging from rare and hard to detect species (i.e., raccoon and spotted skunk) to common detectable species (i.e., cottontail rabbit and mule deer; see Figure 3).

Simulation approach

The occupancy and detection probabilities estimated from the empirical data were used to explore 54 different scenarios for each individual species, using a combination of the number of survey days (occasions: S = (10, 20, 30, 40, 50, 60, 70, 80, 120)) and number of cameras (sites: N = (20, 40, 60, 80, 100, 120)). For each species i, a detection history was created that is N x S, where each site j from j = 1, 2,…N is considered to be occupied or not following a Bernoulli process with probability $\psi_{i.}$; we then determined whether a species was detected or not at occupied sites for each occasion t, from t = 1, 2, …, S, following a Bernoulli process with probability p_i. In total, 1000 sets of detection histories were simulated for each species and each combination of S and N and error was calculated using root mean squared error (RMSE) as:

$$RMSE = \sqrt{E[(\hat{\psi} - \psi)^2]} = \sqrt{Var(\hat{\psi}) + \left(Bias(\hat{\psi}, \psi)\right)^2} \qquad \text{(eqn 1)}$$

Given our simulation setting, the generating and estimating model are equivalent, such that bias will generally be low, except for cases of small-sample bias when survey effort is very low. Thus, the majority of error in RMSE across most scenarios is due to the variance, to the extent that the RMSE can often be considered equivalent to the SE(ψ) (Guillera-Arroita *et al*. 2010; Gardner *et al*. 2010). For each scenario, the RMSE was plotted for the number of sites (cameras) and the length of the sampling period (days). This was repeated for each of the 13 species. To assess the optimal survey design approach, three different RMSE target values were selected representing differing levels of acceptable error; these included RMSE of 0.15, 0.10 and 0.075. For the purpose of our analysis, we weight occasions (days) and sites (cameras) equally to obtain an optimal solution (but see Table S1). The levels of error reflect thresholds used in the wildlife occupancy literature and are considered realistic for determining shifts in occupancy over time and space (MacKenzie & Royle 2005; Guillera-Arroita *et al*. 2010). The optimal survey design (combination of cameras and number of survey days) was then selected as the minimum survey effort required for each species that enabled the estimate of occupancy to be calculated within the desired level of error. Ideally, the lowest level of RMSE is preferred, but this may be logistically unachievable for some species.

Results

Increasing survey effort generally reduced RMSE for all species (Figure 4). However, the optimal combination of the number of sites (motion-activated cameras) and occasions (survey days) varied widely across the 13 species. It was also commonly found that the reduction in RMSE as a result of either increasing the number of cameras or sampling duration would eventually stabilise and would offer limited benefit to further increases in survey effort. Overall, the minimum amount of sampling effort (combination of motion-activated cameras and survey days) required to obtain an acceptable level of error was reduced with increasing daily probability of detection.

Of the species of interest, raccoons had the lowest levels of occupancy coupled with extremely low levels of detection – representing a very rare and hard to detect species in our study area (Figure 3). Even the maximum survey effort (120 motion-activated cameras operating over 120 days) totaling 14400 survey days could not guarantee a reliable occupancy estimate for raccoons; approximately 40% of the simulations failed to numerically converge at a maximum-likelihood estimate due to a lack of data. Spotted skunks were also rare and difficult to detect (Figure 3), however intensive sampling was able to reliably estimate occupancy, requiring 2000 survey days (e.g. a sampling period of 100 days with 20 cameras) for the highest level of acceptable error (RMSE = 0.15) and 5000 survey days for the lowest threshold of error (RMSE = 0.075). These results demonstrate the substantial effort that is required to accurately document the presence of rare and elusive species (Figure 4 and Table 1).

Species that were fairly common with intermediate levels of occupancy but with low detection probabilities (i.e., elk and mountain lion; Figure 3) also required intensive sampling that maximized the number of sites and occasions. When the number of occasions increased from 20 to approximately 80 survey days there was a substantial decrease in RMSE for mountain lion and elk, while estimation error was only further improved by including additional sites to the study design (Table 1 & Figure 4).

For those species with high occupancy (>0.8) and relatively low levels of detection (i.e., coyote and bobcat; Figure 3), the overall survey effort required to achieve a desired level of error is significantly reduced (compared to spotted skunk, mountain lion and elk). Indeed, increasing the number of occasions at comparatively few sites returns a reliable estimate (Table 1 & Figure 4). For example, 10 motion-activated cameras proved sufficient to achieve the desired RMSE of 0.15, 0.10 and 0.075 for bobcats, with the reduction in error achieved by including a greater number of survey days (Table 1). As detection probability increases for more common species (i.e., black bear and gray fox), sampling periods over 40 survey days provide no substantial reduction in associated error and argue against continuing the survey. We found the optimal approach for these common species is to sample between 30-50 sites (cameras) over a period of 40 survey days depending upon the level of error that is acceptable (see Table 1).

For species with comparatively high levels of daily detection (≥0.12; mule deer, cottontail rabbit and virtual species 1-3), there is only a limited reduction in error associated with lengthening the survey beyond approximately 30 days, particularly for species with moderate to high estimates of occupancy (i.e., virtual species 2, mule deer and cottontail rabbit; Figure 3). Precise occupancy estimates for these species can be achieved with relatively few cameras (see Table 1). Nonetheless, improving upon these estimates generally requires adding additional sites (cameras) rather than more survey days (Table 1 & Figure 4). For example, a RMSE of 0.085 can be achieved for cottontail rabbits using only 10 cameras and 20 days of sampling. Further reductions in error cannot be achieved by lengthening the sampling period, with 120 survey days returning an RSME of 0.083 (Figure 4); however error can be substantially reduced by deploying additional cameras (Figure 4).

Virtual species 1 and 3 both have low occupancy estimates but comparatively high probabilities of detection (Figure 3). An intermediate level of survey effort is required in order to achieve the most efficient sampling approach, which depending upon the desired level of precision, balances the number of cameras (20-50) with survey days (20-60; Table 1).

In general reducing RMSE by increasing sampling length depends on the probability of detecting the species at an occupied site at least once over the entire sampling duration. We calculated this probability as p^* ($p^* = 1 - (1 - p)^s$), where p is the daily detection probability and S is the number sampling occasions. When p^* is greater than 0.9 there was very little reduction in RMSE by further increasing the number of sampling occasions (see Table 2).

Our simulation results reveal broad patterns in survey design when using motion-activated cameras that depend upon how easy a species is to detect and how common it is across the landscape (Figure 5). Rare species with low detection require an intensive sampling approach that combines multiple camera sites and occasions to reliably calculate an occupancy estimate, whereas the best strategy for more common species with low levels of detection involves increasing the number of survey days (occasions) at comparatively few sites (≤30 cameras). As detection probability increases, the overall survey effort required to achieve an acceptable level of precision in occupancy is reduced. Species that are detectable but comparatively rare generally require an intermediate number of cameras and greater survey lengths to improve precision, compared with common and detectable species that can be surveyed precisely with relatively few sites and short sampling periods (Figure 5).

Discussion

Reliable indicators that track changes in landscape-to-regional biodiversity are urgently needed, given the global extinction crisis (Mace & Baillie 2007; Butchart *et al*. 2010). Motion-activated cameras can provide scientists and wildlife managers with a very powerful tool for documenting changes in occupancy across a diverse range of species (O'Connell & Bailey 2011; Ahumada, Hurtado & Lizcano 2013), particularly given the advances in storage, reliability and battery life of the latest devices (Jamie 2012). Nevertheless, in common with other ecological monitoring and research programs, successful sampling strategies rely on detailed study design. Indeed, pursuing an optimal survey design allows available time and resources to be maximized, while also providing guidance as to whether the objectives are achievable and justified given potential funding constraints (McDonald-Madden *et al*. 2010). We found substantial differences in optimal survey designs across mammal species from our study area. As MacKenzie & Royle (2005) highlighted, surveying as many sites as possible is not the most efficient approach to reducing overall occupancy estimation error. Instead, obtaining a reliable and efficient occupancy estimate requires tailoring the study design to the species of interest.

The most challenging taxa to develop an appropriate survey design for were the rare and hard to detect species (e.g. raccoons). Even with considerable survey effort it was challenging, if not impossible, to reliably estimate occupancy based on our criteria of RMSE. If the goal of a study is to estimate the occupancy of a rare species that is difficult to detect, it may be necessary to reposition the cameras to target specific taxa or employ multiple methods (e.g., cameras, sign surveys). Even if each method individually has a low probability of detection, the combined effect of all methods incorporated together will be greater, and thus potentially lead to a reliable occupancy estimate. Such an approach can be carried out using multi-scale occupancy models, which allow data to be incorporated from multiple detection methods while permitting estimation of occupancy across different spatial scales (Nichols *et al*. 2008).

Alternatively, for threatened and endangered species it may be more appropriate to forego estimating species occurrence and simply try to determine if the species is present in the area of interest (MacKenzie et al. 2006; Si *et al*. 2014). Researchers can evaluate the probability of photographing a species at least once over a given number of sampling occasions and sites using p^{**} ($p^{**} = 1 - [1 - \psi(1-(1-\mathrm{p})^S)]^N$). For example for a very rare and hard to detect species ($\psi = 0.05$ and $p = 0.05$), the optimal sampling design would be 60 cameras over a sampling period of 80 days to achieve a minimum p^{**} of 0.95. Assuming each camera is $250 and a survey occasion costs $10, a budget of $15,800 would be required to have a 95% probability of detecting the species once (see Table S2). In such situations, active baiting or luring may also be useful (Magoun *et al*. 2011; Hamel *et al*. 2013).

For common and highly detectable species (e.g., cottontail rabbits and mule deer), relatively few motion-activated cameras and survey days are necessary to provide accurate and precise occupancy estimates. As such, rapid assessment surveys could be routinely used to monitor these species relatively inexpensively, while taxa that are comparatively rare across the landscape but yet remain highly detectable (e.g., virtual species 1) require greater survey effort, and are therefore best sampled using an intermediate number of sites and survey days.

Since survey effort involves a trade-off between cameras and sampling length, it is important to note that the financial costs associated with these different scenarios may vary considerably. For example, surveying additional sites may require purchasing more cameras, while increasing the survey duration may require personnel to make additional site visits to keep the cameras functioning properly. The purchasing of additional cameras will likely exceed that of sampling for more days, unless the cost of checking cameras is considerable due to difficulty accessing the study site. Under certain scenarios where the number of sites is limiting the accuracy/precision of the estimate and there is sufficient time for two surveys to be conducted within a designated season, cameras can be set for the necessary period and then moved (e.g., Karanth & Nichols 2002). The number of sites would be doubled with the only extra cost involving the logistics for redeployment rather than equipment purchase. Interestingly, this has also proved an efficient method for measuring species richness (Si *et al*. 2014). It is important to bear in mind that the optimal solution will depend upon the costs associated with camera operation and maintenance versus the costs of procuring cameras (see Table S1, which calculates the optimal approach based on survey cost, where cameras = $250 and surveying an occasion = $10). We report detection probabilities of species relative to 24-hour periods. However, values of detection probability are dependent upon the length of the sampling occasion and researchers will often employ sampling occasions that are measured in weeks rather than days (Ellis, Ivan & Schwartz 2013). Thus if the daily detection probability is 0.03, we can recalculate p using the p^* formula ($p^* = 1 - (1 - p)^s$) such that at 1 week $p = 0.19$, 2 weeks = 0.35, etc. Furthermore, p^* can be used to understand when it is not beneficial to further increase occasions as illustrated in Table 2 (see also Gerber et al. 2014).

The species included in our study cover a diverse range of daily detection probabilities and occupancy estimates representing a broad spectrum of mammals. The findings can therefore be applied to other taxa and ecosystems where cameras are being used to study small to large terrestrial mammals. To determine an optimal study design, we suggest that researchers first investigate the occupancy (i.e. common, moderately common, rare) and detection (i.e. low, moderate, high) characteristics of their target species. Table 1 and Figure 5 can then be used to guide the required sampling effort (number of sites and survey days) for an acceptable level of error. For many mammals, there may already be published literature in which species occupancy and detection probabilities could be obtained. If no prior information is available, short pilot studies can be very effective in obtaining values for occupancy and detection probability, particularly as these values are often highly site specific, or species experts could be consulted to give a rough estimate regarding occupancy and detection probabilities, depending on body size, behaviour and ranging patterns.

It is important to consider that surveying for extended periods to estimate occupancy for species with moderate to high detection probability may not reduce error despite continued survey effort, while also potentially leading to issues associated with the violation of closure (MacKenzie *et al*. 2006). Indeed, deriving a biologically meaningful sampling period (e.g. season) during which occupancy status is assumed not to change may vary depending upon the target species and research question, and is therefore a fundamental consideration for survey design (see Gerber, Williams & Bailey *in press*). Additionally, trade-offs in survey approach will likely be necessary for community-level research, as it is unlikely that a single design will be most efficient for all species. One potential way forward is to initially define the season (timing and scope of inference), and then consider all the species of interest that can be reasonably detected and use the optimum survey effort required to detect all of these taxa (Si *et al*. 2014).

In conclusion, our study investigates the optimal survey effort (sites vs. occasions) required for determining occupancy with a desired level of error across a range of mammalian species using empirical data from motion-activated cameras. The results of our simulation approach clearly highlight that simply increasing survey effort is not the most efficient strategy for obtaining a reliable occupancy estimate. The guidelines presented in the paper are based on the analysis of an empirical dataset collected from a North American study area to provide a real world example that does not solely rely on the simulation of virtual data, while still being directly applicable to research and monitoring programs conducted in other terrestrial ecosystems. We emphasize the use of biological knowledge of the target species coupled with clearly defined *a-priori* objectives that link monitoring or research effort with defined ecological questions or conservation actions (Martin *et al*. 2009). Structured decision theory can be used to formally connect monitoring to decisions that meet objectives outlined by stakeholders in a statistically robust and coherent conservation plan (Conroy *et al*. 2008). Our study also illustrates the value of data simulation approaches for assessing methods and study design before embarking on empirical data collection (Zurell *et al*. 2010; Ellis, Ivan & Schwartz 2013). However, it is not always feasible for practitioners to carry out their own simulation exercises. Thus, research such as ours that can provide broad guidelines when a species of interest can be generally classified as rare or common and easily or difficult to detect will be of great utility to designing effective studies.

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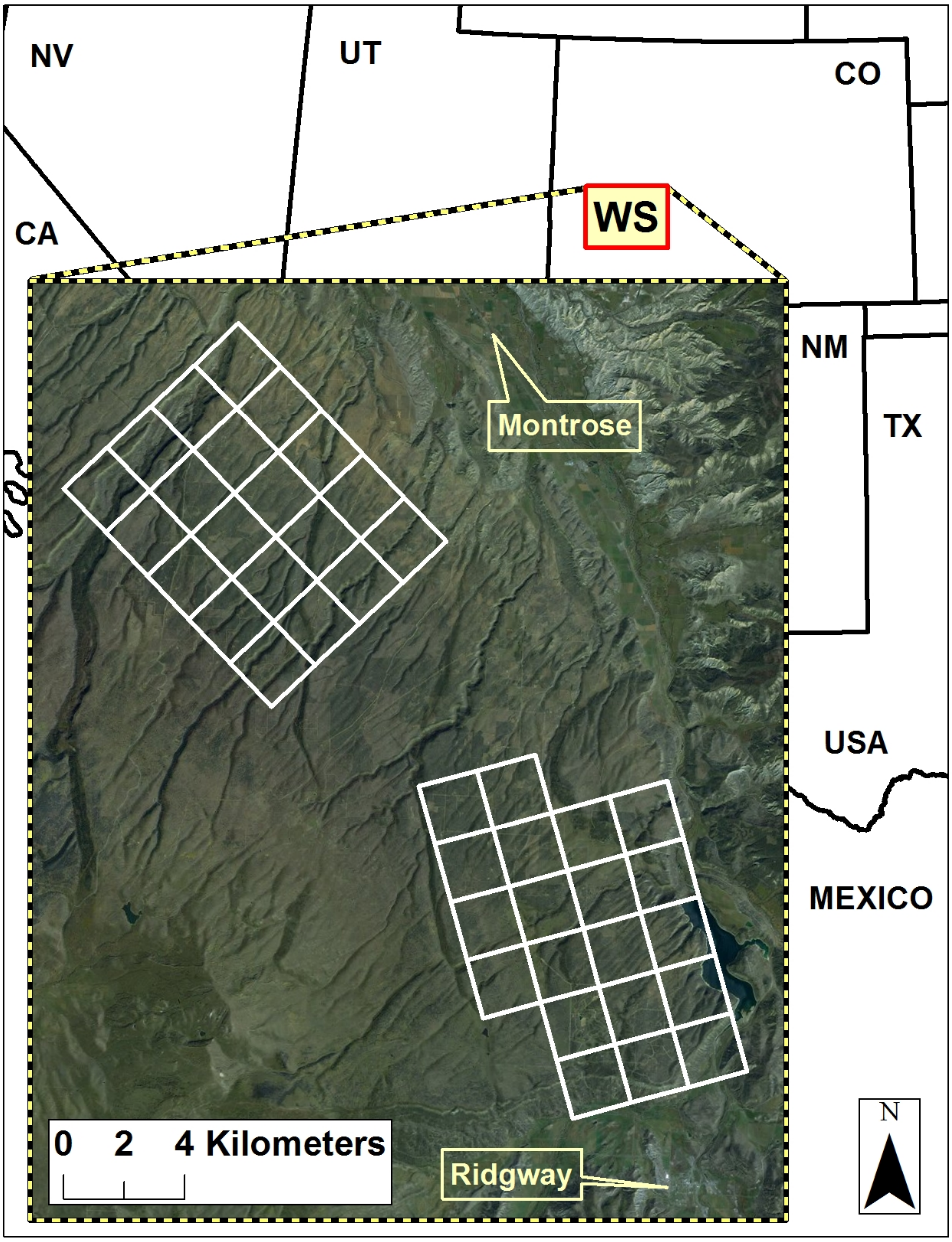
1 

2 **Figure 1.** Location of the study site on the Western Slope, Colorado, USA. The camera survey was

3 completed in 2009 across 40 grid cells across 2 grid areas.

Figure 2. Motion-activated camera images of mammal species included in the study (low to high detection probability). From top left: raccoon, spotted skunk, elk, mountain lion, coyote, bobcat, gray fox, black bear, mule deer and cottontail rabbit.

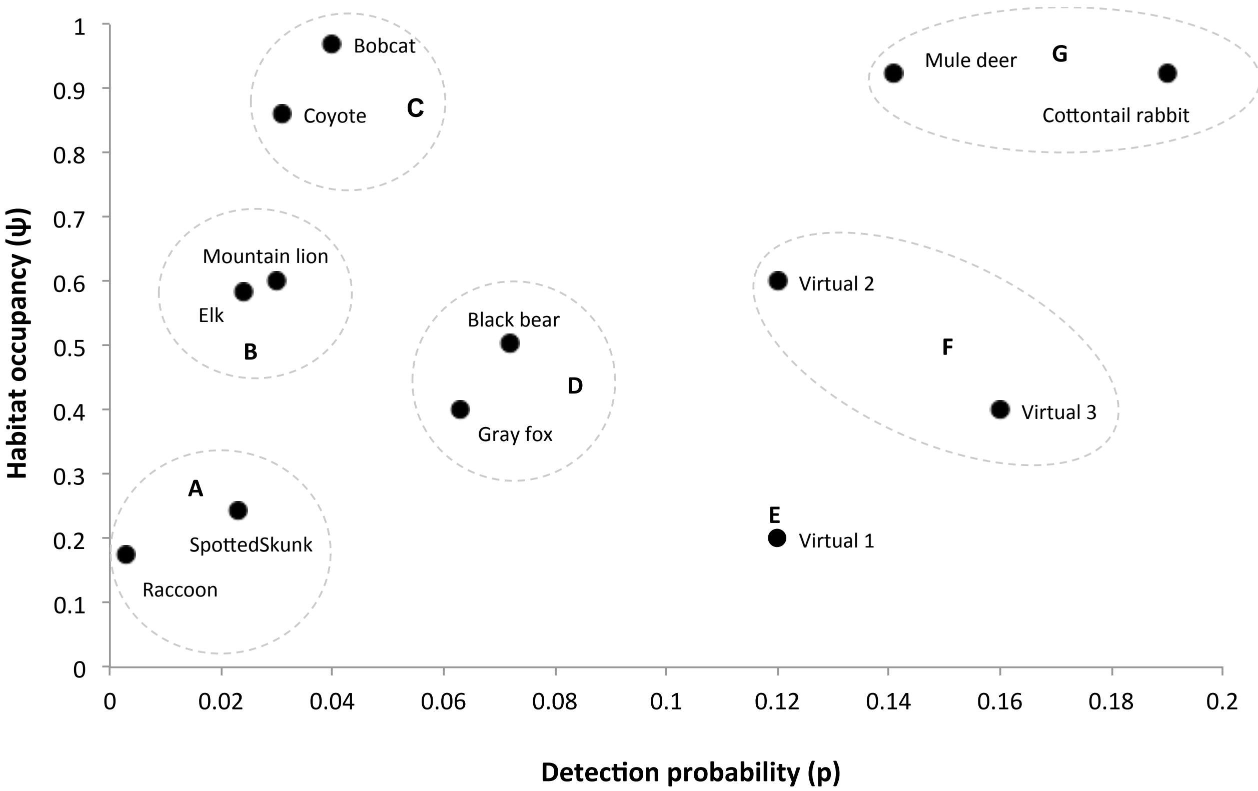
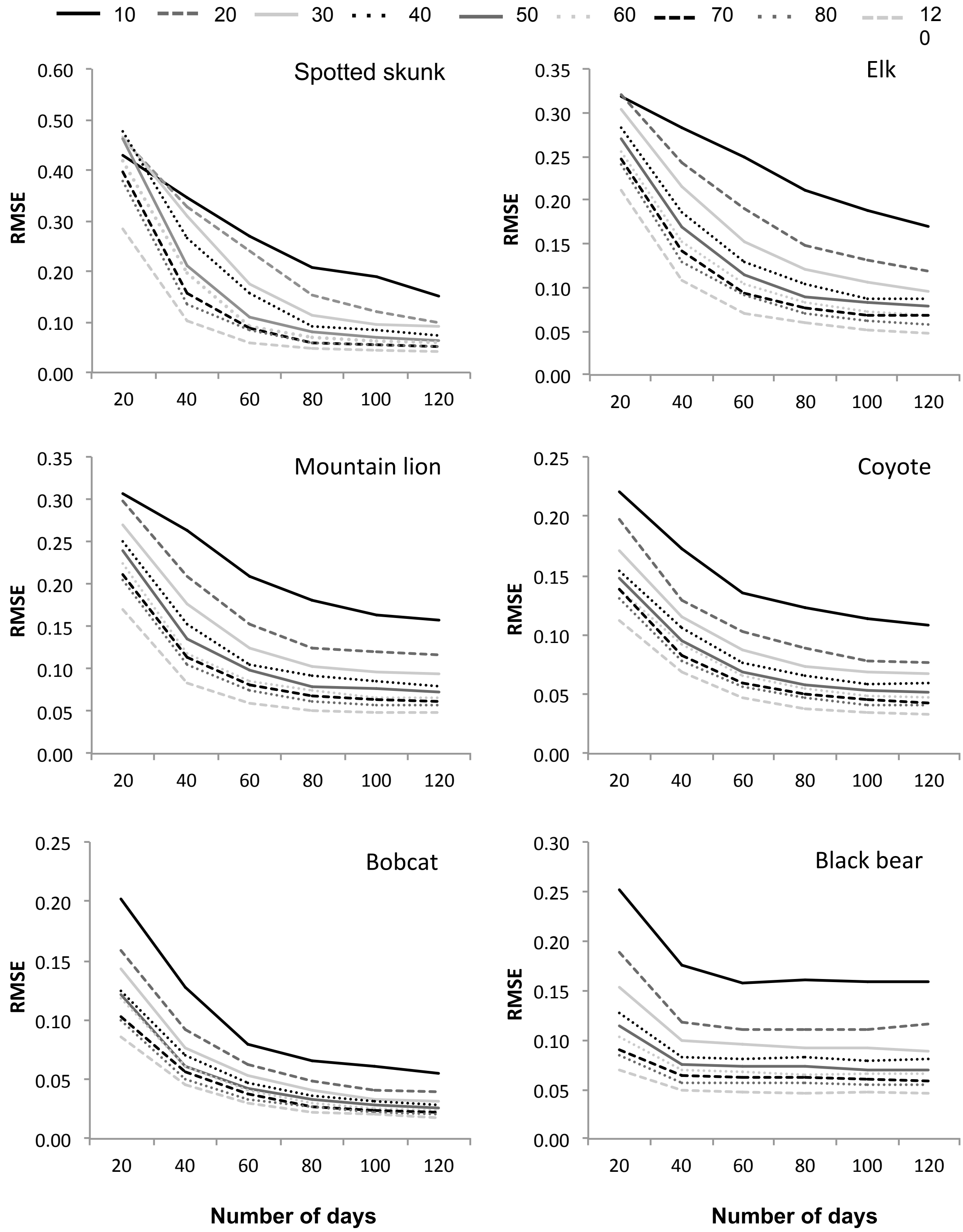


Figure 3. Occupancy estimates and detection probability for 10-mammals and three virtual species that we use to investigate sampling design trade-offs in a simulation exercise. The species are grouped according to common characteristics: A) = low occurrence and low detection probability, B) = moderate occurrence and low detection probability, C) = high occurrence and low detection probability, D) = moderate occurrence and moderate detection probability, E) = low occurrence and high detection probability, F) = moderate occurrence and high detection probability, G) = high occurrence and high detection probability.


10
20
30
40
50
60
70
80
120
Spotted skunk
Elk
Mountain lion
Coyote
Bobcat
Black bear
RMSE
Number of days

1
2

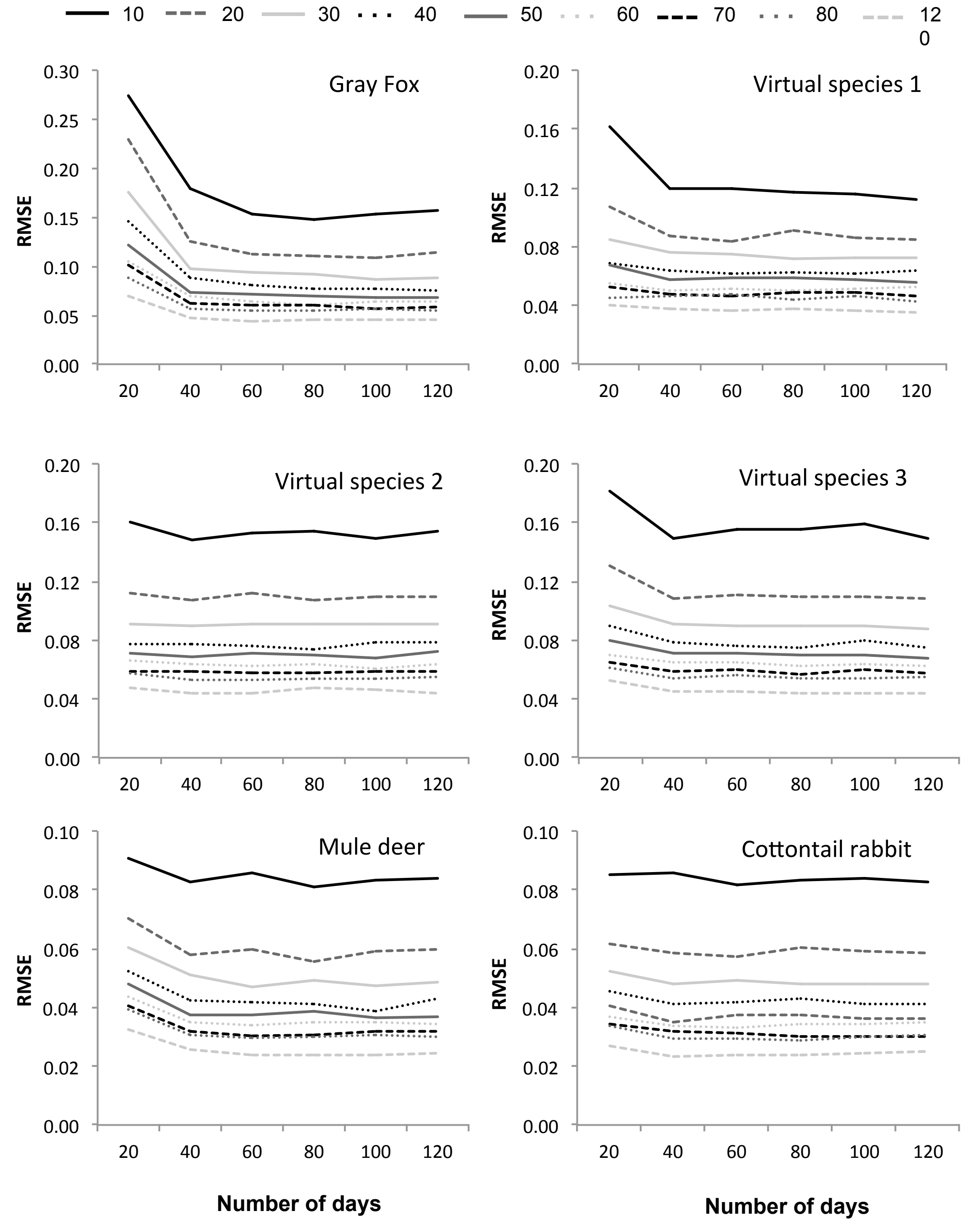


Figure 4.

The influence of survey effort on the error associated with the occupancy estimate (RMSE, root mean squared error), as a function of number of sites (10-120 cameras) occasions (20-120 survey days) and species. Species are presented in order of increasing detection probability (from the top left), with the scale of the y-axis varying between taxa. Raccoons are absent as a reliable estimate could not be achieved due to the lack of data.

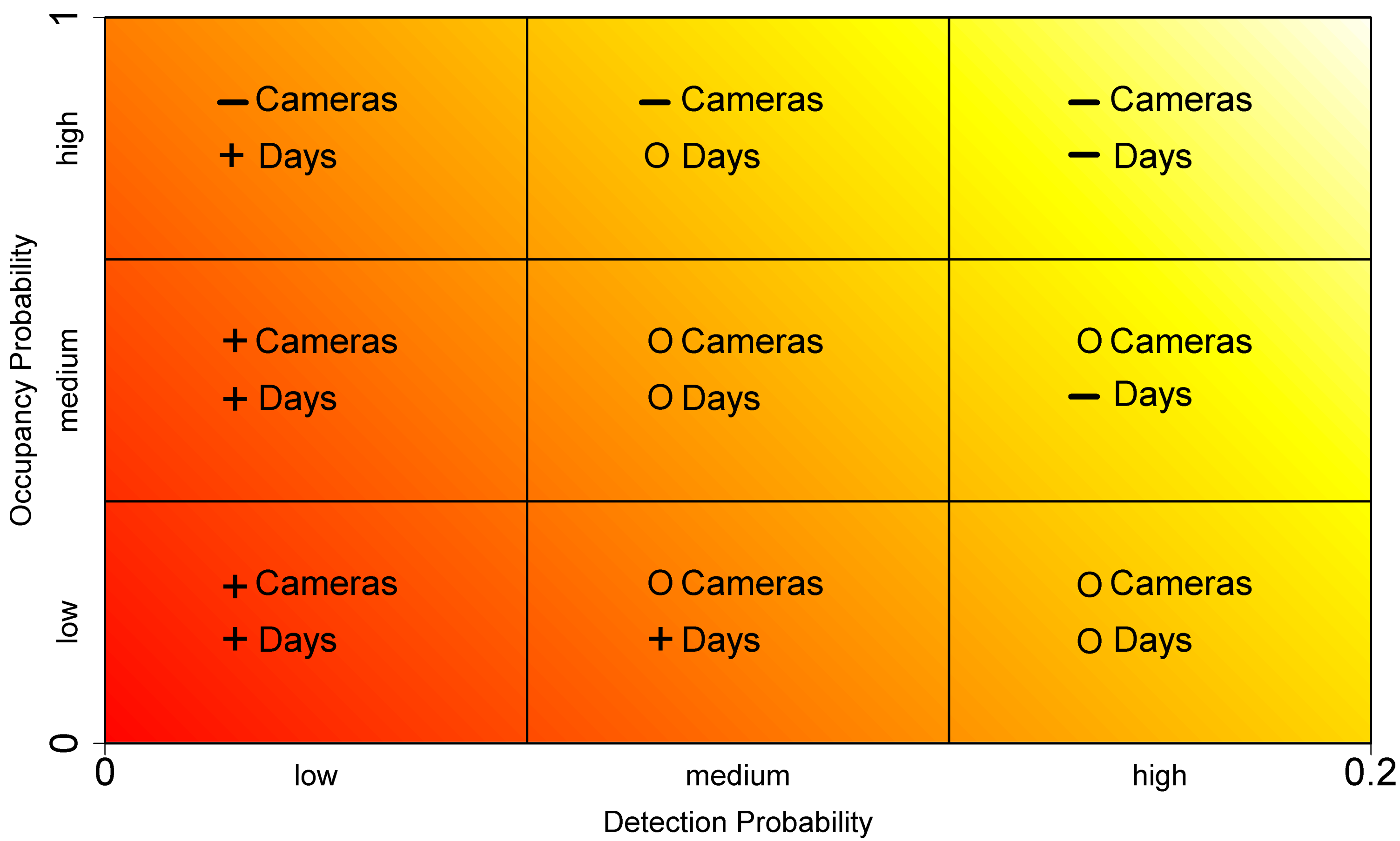


Figure 5. Broad recommendations on survey design for studies exploring occupancy using motion-activated cameras. The symbols indicate high (+), intermediate (O) and low (—) amounts of effort, for the relative number of cameras and survey days to achieve an optimal survey design. From the upper-right to the lower-left, an increasing amount of survey effort is required to reliably estimate occupancy.

Table 1. Optimal survey design for estimating occupancy with three levels of acceptable error, defined by the root mean squared error (RMSE). For the purposes of this example we considered the weighting of cameras versus survey days to have the same cost.

			RMSE 0.15		RMSE 0.10		RMSE 0.075	
Species	Ψ	P	Sites[1] x occasions	Total Survey effort	Sites[1] x occasions	Total Survey effort	Sites[1] x occasions	Total Survey effort
Spotted Skunk	0.245	0.023	20 x 100	2000	30 x 100	3000	50 x 100	5000
Elk	0.585	0.024	20 x 80	1600	30 x 120	3600	60 x 100	6000
Mountain Lion	0.600	0.030	20 x 80	1600	30 x 100	3000	60 x 80	4800
Coyote	0.861	0.031	10 x 60	600	20 x 80	1600	30 x 80	2400
Bobcat	0.970	0.040	10 x 40	400	10 x 60	600	10 x 80	800
Gray Fox	0.400	0.063	20 x 40	800	30 x 40	1200	50 x 40	2000
Black Bear	0.504	0.072	20 x 40	800	30 x 40	1200	50 x 40	2000
Virtual sp. 1	0.200	0.120	20 x 20	400	20 x 40	800	30 x 60	1800
Virtual sp. 2	0.400	0.160	20 x 20	400	30 x 20	600	50 x 20	1000
Virtual sp. 3	0.600	0.120	20 x 20	400	30 x 40	1200	50 x 40	2000
Mule Deer	0.925	0.141	10 x 20	200	10 x 20	200	20 x 20	400
Cottontail Rabbit	0.925	0.190	10 x 20	200	10 x 20	200	20 x 20	400

[1] Sites are the number of cameras and occasions are the number of survey days at each site.

Table 2. The probability (p^*) of detecting a given species at an occupied site at least once over sampling periods of different durations (10-120 occasions). The shading highlights the number of occasions where $p^* \geq 0.9$, and there is only limited improvements in precision to be gained by sampling over longer periods.

Species	**Number of sampling occasions**						
	10	20	40	60	80	100	120
Raccoon	0.03	0.06	0.11	0.16	0.21	0.26	0.30
Spotted Skunk	0.21	0.37	0.61	0.75	0.84	0.90	0.94
Elk	0.22	0.38	0.62	0.77	0.86	0.91	0.95
Mountain Lion	0.26	0.46	0.70	0.84	0.91	0.95	0.97
Coyote	0.27	0.47	0.72	0.85	0.92	0.96	0.98
Bobcat	0.34	0.56	0.80	0.91	0.96	0.98	0.99
Gray Fox	0.48	0.73	0.93	0.98	0.99	1.00	1.00
Black Bear	0.53	0.78	0.95	0.99	1.00	1.00	1.00
Virtual sp. 1	0.72	0.92	0.99	1.00	1.00	1.00	1.00
Virtual sp. 2	0.72	0.92	0.99	1.00	1.00	1.00	1.00
Virtual sp. 3	0.83	0.97	1.00	1.00	1.00	1.00	1.00
Mule Deer	0.78	0.95	1.00	1.00	1.00	1.00	1.00
Cottontail Rabbit	0.88	0.99	1.00	1.00	1.00	1.00	1.00