Power of faecal pellet count and camera trapping indices to monitor mammalian herbivore activity

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ABSTRACT

Context. Monitoring spatial and temporal change in relative abundance using statistically powerful designs is a critical aspect of wildlife management. Many indices of relative abundance are available, but information regarding their influence on statistical power is limited. **Aims.** We compared the statistical power associated with occurrence-based and frequency-based indices derived from faecal pellet counts and camera trapping to detect changes in the activity of five mammalian herbivores. **Methods.** We deployed camera traps and counted faecal pellets in native vegetation subjected to four management treatments in south-eastern Australia. We used simulation coupled with generalised linear mixed models to investigate the statistical power associated with a range of effect sizes for each combination of species, survey method and data type. **Key results.** The index derived from camera frequency data provided the greatest statistical power to detect species' responses and was the only index capable of detecting small effect sizes with high power. The occurrence index from camera trapping did not provide the same level of statistical power. Indices derived from faecal pellet frequency data also detected spatial and temporal changes in activity levels for some species, but large numbers of plots were required to detect medium to large effect sizes. High power to detect medium to large effects could be achieved using occurrence indices derived from pellet presence–absence data, but required larger sample sizes compared to the camera frequency index. **Conclusions.** Both camera trapping and pellet counts can be applied to simultaneously monitor the activity of multiple mammalian herbivore species with differing activity patterns, behaviour, body size and densities, in open and closed habitat. However, using frequency indices derived from camera trapping may improve management outcomes by maximising the statistical power of monitoring programs to detect changes in abundance and habitat use. **Implications.** Frequency indices derived from camera trapping are expected to provide the most efficient method to detect changes in abundance. Where the use of cameras is cost prohibitive, occurrence indices derived from pellet presence–absence data can be used to detect medium to large effect sizes with high power. Nonetheless, the cost-effectiveness of camera trapping will improve as equipment costs are reduced and advances in automated image recognition and processing software are made.

Keywords: *Axis porcinus*, cost-effective, *Macropus giganteus*, mammal, management, monitoring, *Oryctolagus cuniculus*, sampling methods, survey methods, *Vombatus ursinus*, *Wallabia bicolor*.

Introduction

Efficient and reliable methods to monitor spatial and temporal changes in wildlife populations are essential to inform and evaluate management decisions (Månsson et al. 2011) and increasingly, these methods need to be applied in multi-species assemblages (Pfeffer et al. 2018). Simple indices that reflect a change in abundance can be useful for wildlife management, but choices need to be made about which of the alternative indices to use (Engeman 2005). Selection of the most appropriate index can be informed by a formal evaluation of the efficacy and efficiency of candidate methods in the context of

management objectives and resources (Garden *et al.* 2007; Månsson *et al.* 2011; Swan *et al.* 2014; Seidlitz *et al.* 2021).

Indices based on non-invasive sampling methods enable monitoring of animals that are difficult to capture or detect, occur at low densities, or occur in dense vegetation where direct counts are not feasible (Southwell 1989; O'Connell *et al.* 2011). Indices are commonly based on counts of animal sign (Caughley 1977) and faecal pellets are the most obvious sign of the presence of many species. The faecal pellet count method uses pellet density as an index of herbivore abundance and activity (Bailey and Putman 1981). It can also provide an indicator of spatial or temporal habitat use, because pellet density is expected to be proportional to the time spent in a habitat (Hannan and Whelan 1989). Pellet count methods have been validated against known population densities for many species, revealing both linear and non-linear relationships (Barnes 2001; Hayward *et al.* 2005; Forsyth *et al.* 2007; McCann *et al.* 2008; Rönnegård *et al.* 2008; Ariefiandy *et al.* 2013). Faecal pellet counts can be applied simultaneously to multiple species with differing activity patterns and behaviour (e.g. Lunney and O'Connell 1988), and are suitable for use over large areas in most habitats (Mayle *et al.* 1999). Compared with many other monitoring methods, pellet counts are considered to be relatively accurate (Dinerstein 1980; Bailey and Putman 1981), time efficient and cost effective (Caughley 1977), and are frequently used to derive abundance indices for research and management (McCann *et al.* 2008; Forsyth *et al.* 2012).

An alternative sampling method is remote photography using camera traps (O'Connell *et al.* 2011). Camera traps contain heat and motion sensors that activate a camera when animal movement is detected (O'Connell *et al.* 2011). Camera trap data can index changes in population abundance (Rovero and Marshall 2009; Bengsen *et al.* 2011; Latham *et al.* 2012), activity patterns (Hossain *et al.* 2016) and habitat use (Augustine 2004; Claridge *et al.* 2004). Like pellet counts, camera traps can simultaneously monitor multiple species (Wacher and Attum 2005) in many habitat types, under varied environmental conditions (Vine *et al.* 2009). Camera traps are easy to use and, once deployed, do not require manual operation, allowing remote sampling over extended periods (Bridges and Noss 2011). Compared to a number of traditional methods, camera traps are relatively effective at detecting mammal species (Silveira *et al.* 2003; De Bondi *et al.* 2010; Paull *et al.* 2012; Swan *et al.* 2014; Wearn and Glover-Kapfer 2019), and are increasingly used for population monitoring (Karanth *et al.* 2004; Nichols *et al.* 2011). Importantly however, camera trapping does not always outperform traditional survey methods, providing lower or similar probabilities of detection and estimates of species richness and composition for some faunal groups (Silveira *et al.* 2003; Gompper *et al.* 2006; Espartosa *et al.* 2011; Seidlitz *et al.* 2021). Camera trapping also requires a substantial investment in equipment (Silveira *et al.* 2003)

and time for post-processing of data (Latham *et al.* 2012) compared to traditional methods such as pellet counts.

Studies comparing camera trapping and pellet counts for mammalian herbivores suggest that indices from the two methods can be correlated (Lucherini *et al.* 2009; Li *et al.* 2014; Morgan *et al.* 2018*a*) but camera trapping can index activity in situations where pellet counts are too low to be useful (Kuijper *et al.* 2009), and can more accurately estimate density (Roberts 2011). For carnivores, studies have demonstrated that camera and pellet-based indices of abundance were correlated for some species (Garrote *et al.* 2014) but not others (Gompper *et al.* 2006), likely influenced by variation in factors such as densities, ranging behaviour and the ability to identify individuals (Barea-Azcón *et al.* 2007; Jhala *et al.* 2011). While these studies provide general support for agreement between camera and pellet-based indices, they are limited to a small number of species and environments.

Assessment of the ability of monitoring methods to detect changes in animal populations also requires consideration of the type of data collected (Bengsen *et al.* 2014). Count data are common in ecological studies (Fordyce *et al.* 2011) and are used in wildlife monitoring to measure spatial and temporal variation in abundance (Archaux *et al.* 2012). Faecal pellet indices are usually based on counts (Mayle *et al.* 1999) and camera indices calculated as frequencies (e.g. counts of the number of observations standardised over time; Kawanishi *et al.* 1999; Negrões *et al.* 2010), but collection of count data is resource intensive (Gompper *et al.* 2006; Torney *et al.* 2019). An alternative is to collect species detection versus non-detection (i.e. presence–absence) data, which can be used to measure the probability of occurrence at a site. Presence–absence data are widely used for monitoring (Wintle *et al.* 2005; Steenweg *et al.* 2016) and may be easier to collect than count-based data enabling improvements in efficiency (Nichols *et al.* 2011). For example, in the context of remote camera surveys and faecal pellet counts, deriving presence–absence data sets removes the need to process all images or count all pellets, likely saving substantial time and cost. Despite this there is little information about the relative performance of count and presence–absence data for monitoring abundance change.

To ensure monitoring programs are rigorous and to optimise return on effort and expenditure, it is essential to evaluate the capacity of monitoring methods to detect change (Smart *et al.* 2004; Field *et al.* 2007). However, little information is available to compare the relative performance of indices from faecal pellet count and camera trapping methods, based on presence–absence and count data. We conducted a field-based comparison of faecal pellet counts (both faecal accumulation and faecal standing crop) and camera trapping. Our objective was to compare the statistical power of these methods, using indices derived from both occurrence (presence–absence) and frequency (count) data, to detect spatial and temporal changes in the relative activity

levels of five mammalian herbivore species that differed in body size, behaviour, activity patterns and densities.

Materials and methods

Study area

We conducted the study on Yanakie Isthmus (38°53′S; 146°14′E), Wilsons Promontory National Park, Victoria, Australia. Indices of herbivore activity inform decisions regarding management of grazing pressure at this site as part of an adaptive management approach to the restoration of Coastal Grassy Woodland invaded by a native woody shrub, coast tea-tree *Leptospermum laevigatum* (Morgan *et al.* 2018b).

The study area consisted of 200 ha of Coastal Grassy Woodland containing dunes and inter-dune swales with an open structure. *L. laevigatum* biomass in the shrub and canopy layers had been reduced using mechanical slashing (Davis *et al.* 2016) 4 years prior to the study, and/or prescribed burning in December 2012, 4 months prior to the study. The area also contained swales with a partially open structure, in which *L. laevigatum* was regenerating following prescribed burning 4 years prior to the study.

We focussed on five mammalian herbivore species (eastern grey kangaroo *Macropus giganteus*, swamp wallaby *Wallabia bicolor*, common wombat *Vombatus ursinus*, hog deer *Axis porcinus* and European rabbit *Oryctolagus cuniculus*) that require monitoring to guide management of grazing impacts (Morgan *et al.* 2018b). These species differed in behaviour, activity patterns and body size (ranging from 1 kg to 45 kg; Menkhorst and Knight 2011) and densities (Davis *et al.* 2018).

Experimental design

We tested camera trapping and faecal pellet counts concurrently using the same experimental design and sampling locations to maximise comparability of data collected using the two survey methods. We counted pellets in circular 3-m radius plots ($n = 201$) to estimate faecal standing crop (FSC; Mayle *et al.* 1999) from 9 April to 2 June 2013, and simultaneously cleared pellets from plots in preparation for estimation of faecal accumulation rate (FAR; Mayle *et al.* 1999). We conducted the FAR survey from 15 to 18 July, approximately 3 months after the mid-point of the plot clearance period, with the accumulation period for plots ranging from 80 to 97 days. We deployed cameras at a subset of the 3-m radius plots ($n = 36$) for the duration of the FSC and FAR survey periods (9 April–18 July). We placed cameras on the northern boundary of plots so that the detection zone encompassed most of the plot but moved cameras 5 m from the northern boundary if vegetation clipping in the detection zone was required, to ensure that clipping did not interfere with the test of pellet counts in dense regrowth.

We used both pellet counts and camera trapping to sample 12 swales (0.18–4.18 ha; $\bar{x} = 1.74$ ha) separated by ~0.05–2 km because managers aimed to restore open vegetation and were interested in monitoring herbivore responses to management interventions at this scale. To test monitoring methods in vegetation with varied structure, which we expected would result in spatial differences in herbivore activity, we sampled four treatments (three swales per treatment): (1) *slashed unburnt* – swales opened by mechanical slashing alone; (2) *slashed burnt 2012* – swales opened by mechanical slashing and burning; (3) *unslashed burnt 2012* – swales opened by burning alone in 2012; and (4) *unslashed burnt 2009* – swales opened by burning alone in 2009, but which had partially closed following vegetation regeneration (Fig. 1). All swales were flat to slightly undulating. Slashed unburnt swales were predominantly open in structure, with high (60–70%) ground layer vegetation cover and small patches of dead fallen *L. laevigatum* branches (20–30% cover). Slashed burnt 2012 swales were similarly open in structure with less (30–50%) ground layer vegetation cover, and the remainder of the ground surface was bare. Unslashed burnt 2012 swales were largely open but dominated by dense burnt *L. laevigatum* stems in places, the ground was predominantly bare, and there was little (5–30% cover) ground layer vegetation. Unslashed burnt 2009 swales had dense ground (80–90%) and shrub (0.6–2 m; 40–90%) cover dominated by *L. laevigatum*. Vegetation cover values were estimated visually within each treatment.

To select sampling locations within each swale we applied a 10-m buffer around swale boundaries to reduce edge effects, then randomly selected locations from 20-m grid intercept points generated by geographic information system (GIS) mapping. We allocated plots to swales in approximate proportion to area: slashed unburnt ($n = 50$); slashed burnt 2012 ($n = 59$); unslashed burnt 2012 ($n = 60$); and unslashed burnt 2009 ($n = 32$). For camera traps, we divided samples equally among swales ($n = 9$ per treatment) to ensure that each swale was sampled in the event of camera malfunction.

Camera trapping

We used Reconyx HC600 Hyperfire H.O. covert infrared cameras, which have passive infrared (PIR) capability to detect the difference between the ambient air temperature and the animal's body temperature. We used a passive survey approach (i.e. no lure), so that herbivore behaviour was not altered (Meek *et al.* 2012).

We standardised camera placement and settings to minimise differential detection probabilities (O'Brien 2011) and maximise detection of target species. We mounted cameras on wooden stakes at a height of 50 cm, set horizontally with the PIR sensor aimed 6 m away at the smallest species core body zone (i.e. ~20 cm above the ground) (Meek *et al.* 2012). Cameras were set to high sensitivity and three images per trigger with no delay, facing south to improve
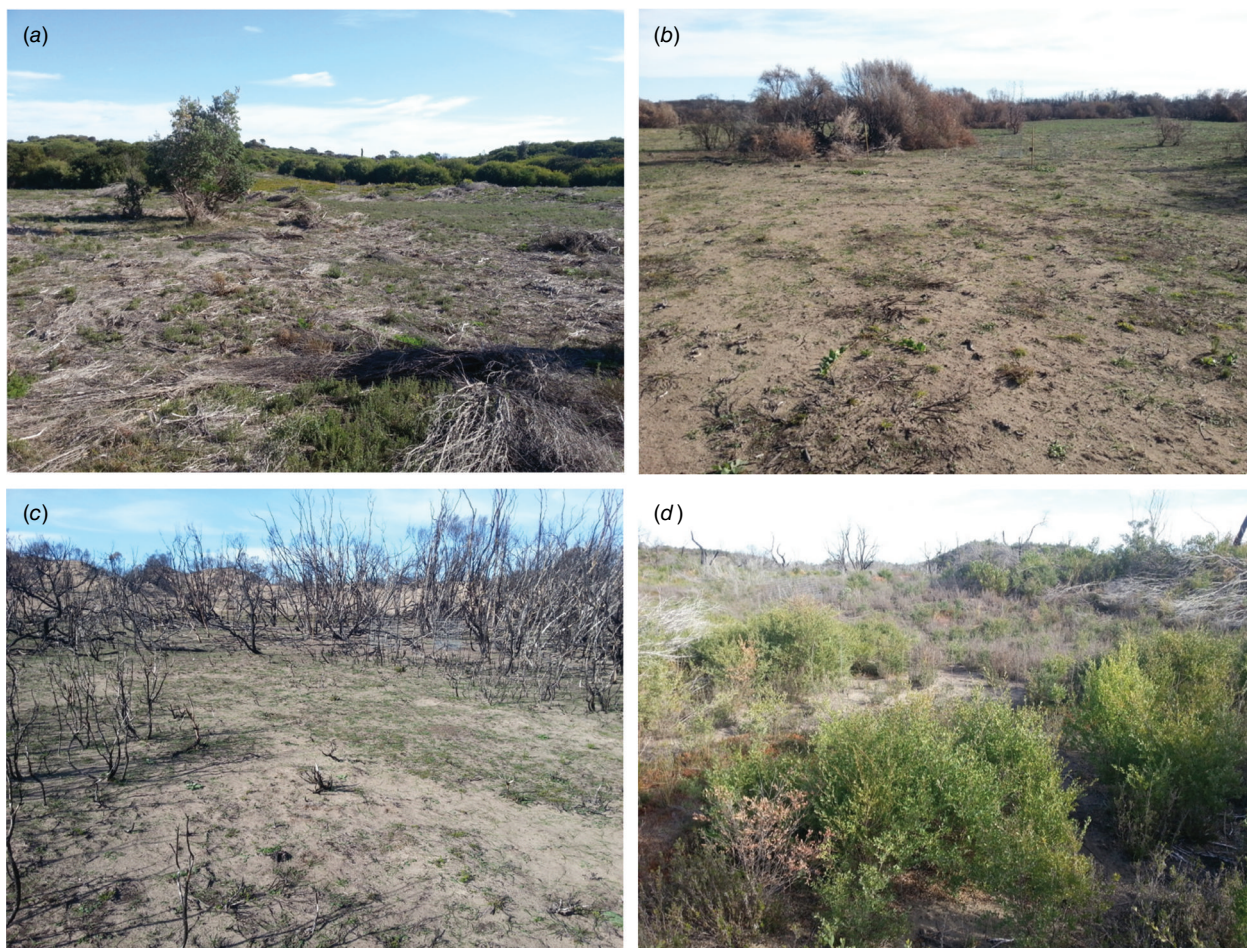
Fig. 1. Photographs demonstrating treatment variation within the study site, Yanakie Isthmus, Wilsons Promontory National Park, Victoria, Australia, 2013: (*a*) slashed unburnt swales; (*b*) slashed burnt 2012 swales; (*c*) unslashed burnt 2012 swales; (*d*) unslashed burnt 2009 swales.

image quality and prevent triggering by direct sunlight (Meek *et al.* 2012).

To allow comparisons across open and closed habitats we standardised camera detection zone size by placing cameras on flat ground with a post 6 m in front of cameras to mark the limit of the detection zone. In addition, we clipped vegetation to 15 cm above the ground using a brush-cutter within the conical shaped detection zone extending 6 m in front of the camera and 40° either side of that central line of sight.

For each day during the survey period, we recorded whether each camera detected the target species within the 6-m detection zone. For marsupials, we counted young-at-foot, but not pouch young, based on the assumption that only young-at-foot contribute directly to grazing pressure and because detectability of pouch-young would be highly variable.

Faecal pellet counts

We used faecal accumulation rate (FAR) counts to reduce the lag between changes in animal activity and the ability of faecal pellet counts to detect that change (Davis and Coulson 2016), and reduce bias associated with pellet decay (Campbell *et al.* 2004). In addition, we used faecal standing crop (FSC) counts, which can provide a precise index of changes in herbivore activity (Mayle *et al.* 1999).

We counted individual pellets for the three marsupial species (eastern grey kangaroo, swamp wallaby, common wombat), given their small pellet group sizes and difficulties that can arise in distinguishing groups (Southwell 1989). We counted pellet groups for hog deer, because the number of pellet groups produced daily is a more reliable index of deer density than the number of individual pellets produced (Smith 1964), and counting is more efficient for species that deposit large numbers of small pellets. Following Hickling (1986), we defined hog deer pellet groups as ≥6 pellets of the same defecation, with at least one visible above the ground litter. Rabbit pellets are also commonly deposited in groups, so we also applied this definition to rabbit pellet groups. If rabbit pellet groups could not be defined within latrines containing large deposits of pellets,

we approximated groups as consisting of *c*. 20 pellets (Davis and Coulson 2016). We counted pellet groups if >50% of pellets fell inside the plot (Mayle *et al.* 1999).

We identified pellets based on size, shape and colour (Triggs 2003). We systematically searched plots for pellets by pushing the vegetation aside, but not disturbing the litter except to look for additional deer or rabbit pellets when one was visible above the litter (Hickling 1986).

Statistical analyses

We used faecal pellet and camera trapping data to index spatial and temporal changes in species activity. Two activity indices were derived from each method, using occurrence (presence–absence) and frequency (count) data (Table 1). Because statistical power to detect change is inversely related to the variance of the response variable, we undertook pre-liminary analyses to explore the variance associated with different forms of the camera trapping frequency index, as numerous options exist (Burton *et al.* 2015). We selected a camera frequency index based on counts of the number of days on which each species was recorded as present as a proportion of the maximum number of survey days because it resulted in lower variance associated with outliers (large numbers of images at some plots) and overdispersion than did other options examined. Similar approaches using indices based on the number of days of detection have been applied by others (e.g. Geary *et al.* 2018; Nalliah *et al.* 2022).

We compared indices using data collected during the same sampling periods because herbivore activity patterns may change seasonally. FSC counts were conducted at the end of autumn to predominantly reflect autumn activity levels (Davis and Coulson 2016), whereas FAR counts reflected winter activity levels. We then subsampled camera data from two 14-day survey periods and compared camera and FSC data collected in autumn between 9 April and 2 June, and camera and FAR data collected in winter between 30 June and 18 July.

We used generalised linear mixed models (GLMMs) and simulated datasets to investigate the statistical power associated with a range of effect sizes for each combination of species, survey method and data type. Initially we built GLMMs for each species with treatment included as a fixed effect and swale specified as a random effect to accommodate variance associated with the spatial nestedness of the study design resulting from sampling of plots within swales (Zuur *et al.* 2009). We also included an individual-level random effect to correct for overdispersion where necessary (Zuur *et al.* 2009). Models of species' occurrence and frequency indices (Table 1) were applied with a logit link function and binomial errors, allowing us to standardise effect-size tests across all data types. The rabbit FSC frequency index model failed to converge so we excluded it from the analysis.

Power analyses were conducted in R version 3.6.3 (R Core Team 2020) using the package simr, which calculates power for GLMMs using Monte Carlo simulation (Green and MacLeod 2016). Calculations involved three steps: (1) new response-variable values were simulated 1000 times based on the GLMM; (2) the model was fitted to the simulated response data; (3) a likelihood ratio test was applied to the simulated fit. The power estimate was derived from the number of successes and failures to detect a statistically significant effect ($P \leq 0.05$) in step 3.

For each combination of species, survey method and data type, we adjusted the effect size of interest using the fixef function in the simr package (Green and MacLeod 2016). Retrospective observed power calculations, where the target effect size is determined by the data, can generate misleading results (Hoenig and Heisey 2001), so we considered a range of ecologically plausible effect sizes representing small (0.10), medium (0.30) and large (0.50) differences in the probability of occurrence (occurrence indices) or proportions (frequency indices) (Table 2). Greater statistical power is required to detect a given effect size at the extreme ends of the binomial distribution (for example, a difference in the

Table 1. Activity indices derived from faecal accumulation rate (FAR) counts, faecal standing crop (FSC) counts and camera trapping data to index spatial and temporal changes in species activity.

Survey method	Data type	Description
FSC	Occurrence	Probability of occurrence based on the presence–absence of pellets (marsupials) or pellet groups (deer and rabbit) during the FSC survey period
	Frequency	Counts of the number of pellets or pellet groups during the FSC survey period as a proportion of the maximum count per species
FAR	Occurrence	Probability of occurrence based on the presence–absence of pellets (marsupials) or pellet groups (deer and rabbit) at the end of the accumulation period
	Frequency	Counts of the number of pellets or pellet groups at the end of the accumulation period as a proportion of the maximum count per species
Camera trapping	Occurrence	Probability of occurrence based on the presence–absence of each species over a 14-day period
	Frequency	Camera frequency index (counts of the number of days on which each species was recorded as present as a proportion of the maximum number of 14 days)

Table 2. Scenarios (species, method, sampling effort, data type and effect size) used for power analysis.

	Categories/scenarios
Data type	Stage 1: Cameras, faecal standing crop
	Stage 2: Cameras, faecal accumulation rate
Species	Eastern grey kangaroo, swamp wallaby, common wombat, hog deer, rabbit
Response variables	Presence–absence, frequency (for cameras data, this was the number of days a species was detected out of the total number of days the camera was deployed; for FSC and FAR data, this was the number of pellets counted in a plot relative to the maximum number of pellets recorded in plot)
Effect size	Small (0.10): centre (0.55–0.45), upper end (0.90–0.80)
	Medium (0.30): centre (0.65–0.35), upper end (0.90–0.60)
	Large (0.50): centre (0.75–0.25), upper end (0.90–0.40)
Number of plots per treatment (fixed effect)	5, 10, 20, 40, 60, 80, 100, 120, 140, 160, 180, 200, 220, 240, 260, 280, 300
Total number of swales (random effect)	5, 10, 20, 40, 60, 80, 100

probability of occurrence between 0.2 and 0.1, or between 0.9 and 0.8) relative to the centre (a difference between 0.55 and 0.45), so we examined each of three effect sizes (small, medium and large) at both the centre and upper end of the range. To investigate the trade-off between sample size and power, we used the powerCurve function in simr to estimate power associated with a sample size of 0–300 plots.

Results

Species' responses to time and treatment were generally similar for the alternative activity indices (Supplementary Figs S1, S2). However, the survey effort required to detect significant effects of treatments during both autumn and winter varied between indices from different survey methods, and between indices derived from frequency and occurrence data (camera trapping compared to FSC; autumn: Fig. 2) and (camera trapping compared to FAR; winter: Fig. 3).

Indices based on frequency

For all species, the activity index derived from camera frequency data was able to detect treatment effects with greater power using fewer plots than the other activity indices (Figs 2, 3). For example, in considering power resulting from up to 300 plots, camera frequency data delivered the only index capable of detecting small effect sizes with high power, and fewer than 50 plots were sufficient to detect medium to large effect sizes for most species using this index.

In contrast to the activity index derived from camera frequency data, power to detect small effects using indices derived from pellet count frequency data was low (Figs 2, 3). Power associated with the FSC frequency index was consistently low, with greater than 100 plots required to detect all but large effect sizes for most species (Fig. 2). For the FAR

frequency index, power to detect medium to large effects varied among species (Fig. 3). FAR frequency data had high power to detect large effects in swamp wallaby and wombat activity levels (Fig. 3). However, the number of plots required to detect medium to large effect sizes for most species was similarly large (>100) to that required for the FSC frequency index, and for species such as deer, even very large sample sizes (>300 plots) were not adequate to detect large effect sizes with high power (Figs 2, 3).

### Indices based on occurrence

Occurrence indices from the three alternative methods performed similarly, requiring fewer plots than pellet count frequency indices, but a greater number of plots than the camera frequency index to detect small–large effects for most species (Figs 2, 3). Overall, power to detect small effects was low for indices derived from occurrence data. However, there was interspecific variation in the number of plots required to detect effects using occurrence indices, and the performance of the camera occurrence index varied over time. Medium–large effect sizes could be detected with high power for several species using occurrence indices: FSC occurrence index for all species except rabbit; and FAR and camera occurrence indices for kangaroo, deer and rabbit. Further, small effects sizes could be detected with medium to high power for some species using pellet occurrence indices if a large number of plots was used.

Discussion

Increasingly, it is recognised that the objectives of monitoring programs can be met using indices of relative abundance (Engeman 2005; Johnson 2008), yet there is limited information on the performance of different indices to help
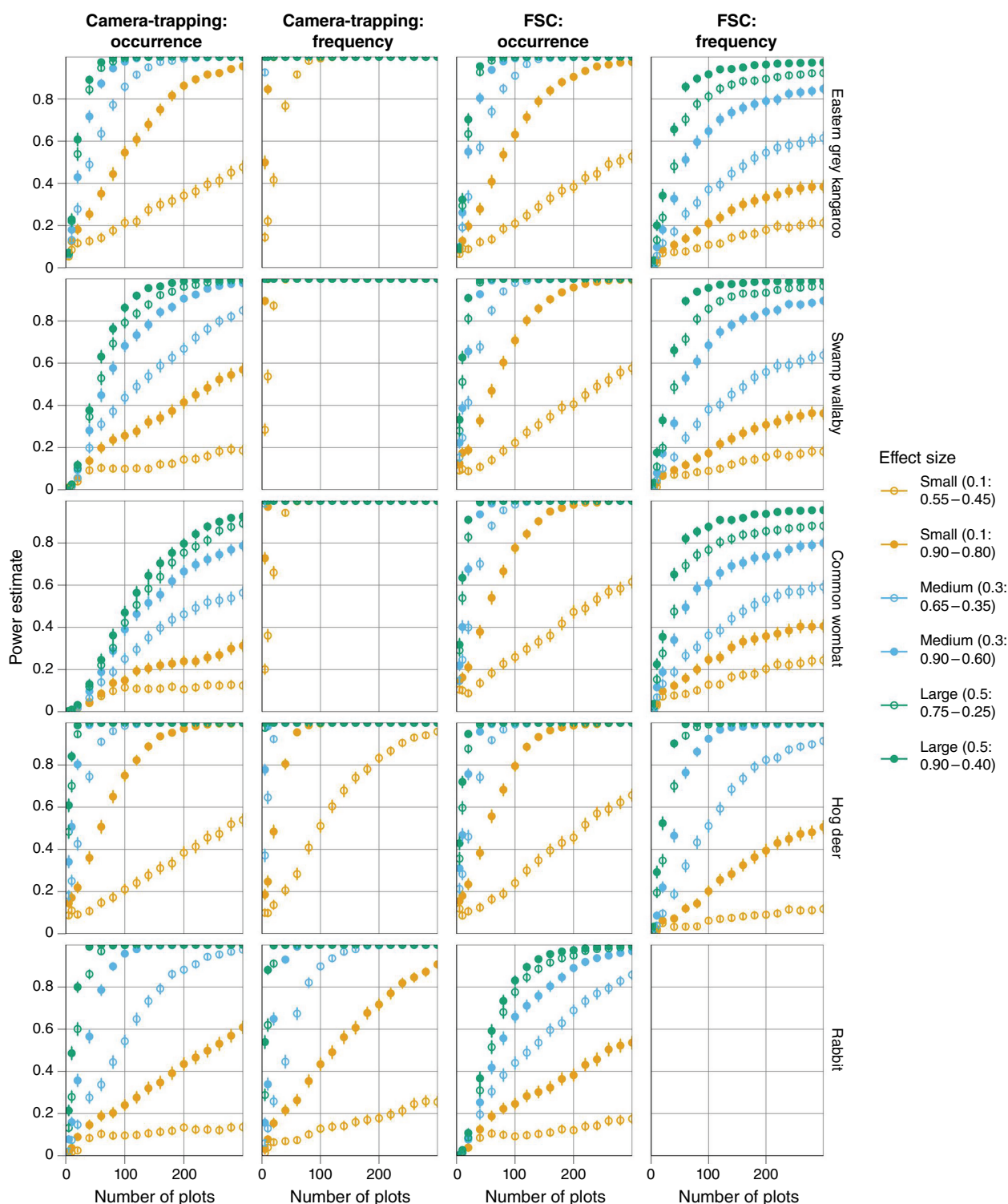
Fig. 2. Statistical power for three effect sizes (small, medium and large) at both the centre and upper end of the binomial distribution. Power was calculated using Monte Carlo simulation for combinations of species (eastern grey kangaroo, swamp wallaby, common wombat, hog deer, rabbit), data type (Faecal Standing Crop and camera activity indices derived from occupancy and frequency data collected at Wilsons Promontory National Park during autumn; 9 April–2 June 2013) and response variable modelled using generalised linear mixed models (GLMM). No output was obtained for the rabbit activity index derived from Faecal Standing Crop frequency data due to computational problems.
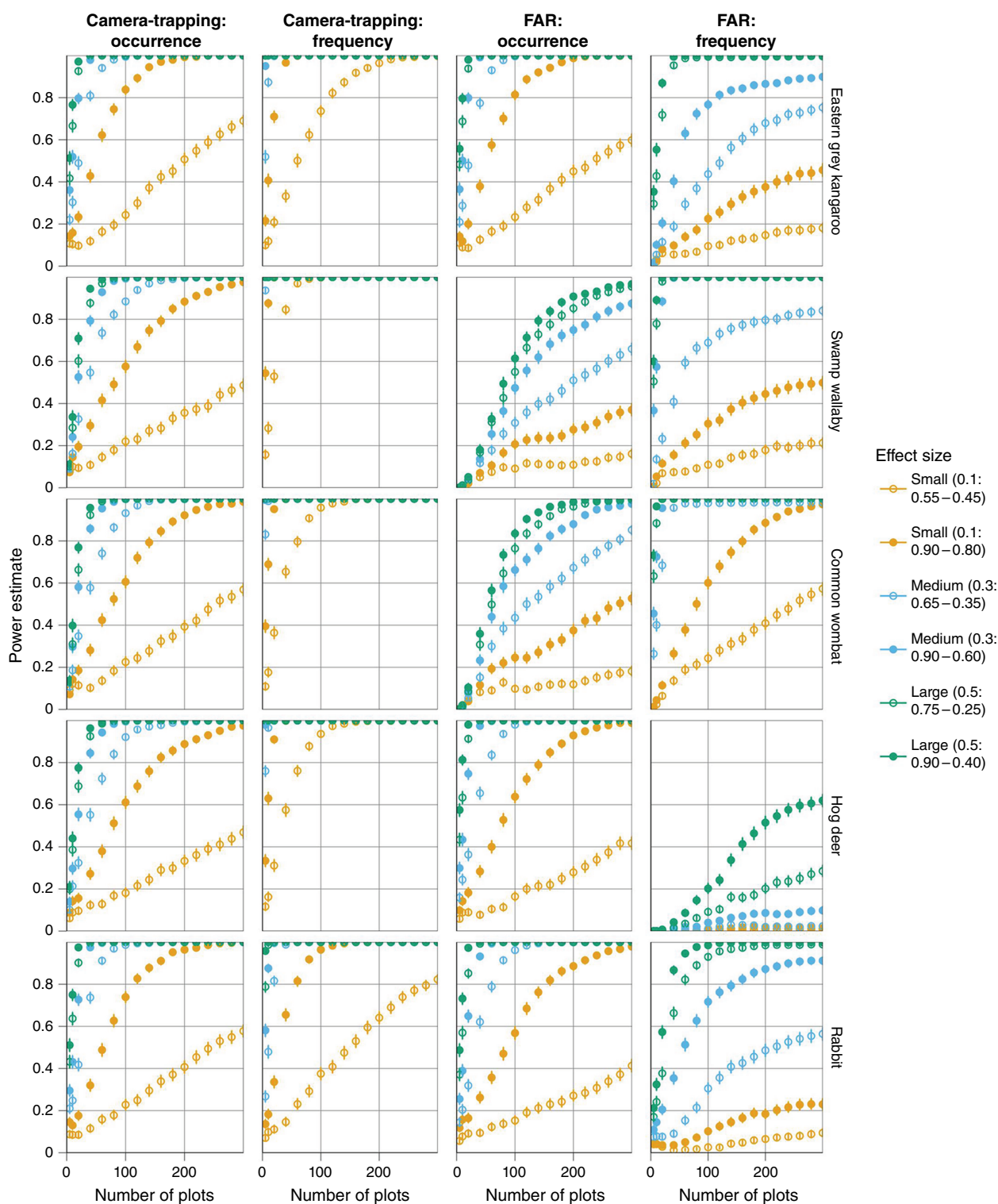
Fig. 3. Statistical power for three effect sizes (small, medium and large) at both the centre and upper end of the binomial distribution. Power was calculated using Monte Carlo simulation for combinations of species (eastern grey kangaroo, swamp wallaby, common wombat, hog deer, rabbit), data type (Faecal Accumulation Rate and camera activity indices derived from occupancy and frequency data collected at Wilsons Promontory National Park during winter; 30 June–18 July 2013) and response variable modelled using generalised linear mixed models (GLMM).

managers choose between the range of survey methods and metrics available. Our study compared the statistical power of faecal pellet count and camera trapping methods for detecting changes in the relative activity levels of mammalian herbivores using indices based on frequency and occurrence data. We demonstrated that an activity index derived from camera frequency data detected treatment effects with greater power and fewer plots compared to the other activity indices and was the only index capable of detecting small effect sizes with high power.

Our results support the work of Latham *et al.* (2012) who showed that medium to large changes in rabbit numbers could be detected using count data from small camera sample sizes and short deployment times with good statistical power. In line with others (Silveira *et al.* 2003; Balme *et al.* 2009; Roberts 2011) we, therefore, advocate camera trapping as providing high power and rigour for monitoring change in relative abundance in a range of species. Some studies have noted that a combination of methods may be required to ensure that different species are detected (Catling *et al.* 1997; Swan *et al.* 2014), yet our camera set-up was effective for detecting species with different body sizes and behaviours, maximising the monitoring potential of this method (Engeman 2005).

While the camera-based frequency index gave the highest statistical power, it is important to evaluate monitoring methods relative to their cost (Perkins *et al.* 2013). We did not undertake a cost-benefit analysis because costs vary widely between projects due to factors such as travel times and whether paid staff or volunteers conduct field work, and because costs change over time and among regions. Nonetheless, it is known that the initial outlay required for camera trapping equipment is greater than that required for low-tech sign survey methods (Gompper *et al.* 2006; Lucherini *et al.* 2009; Garrote *et al.* 2014; Paton *et al.* 2021). This can make camera trap monitoring cost prohibitive if equipment costs cannot be spread across multiple projects, even with decreases in the cost of camera equipment and the time involved in post-processing of images (Latham *et al.* 2012) as camera trapping technology such as automated image recognition and processing software advance (Norouzzadeh *et al.* 2018; Weinstein 2018). Therefore, when cameras cannot be purchased or borrowed, but labour resources are readily available and detection of medium to large effect sizes is adequate to meet monitoring objectives, indices derived from FAR or FSC occurrence data (depending on the species) are more appropriate choices. Moreover, while detection of small effect sizes may be essential for some programs (e.g. threatened species monitoring) (Smart *et al.* 2004), the small effect sizes detected using camera trapping frequency indices may not be ecologically meaningful or relevant to management of many wildlife populations (Di Stefano 2003). Other indices may, therefore, provide adequate statistical power to detect species' responses with equivalent effort and lower costs.

All six indices considered told a similar ecological story, and any could be applied to monitor herbivore activity in open or closed habitat. Occurrence data are appealing because they are relatively simple and cost-effective to collect (De Bondi *et al.* 2010; Steenweg *et al.* 2016) compared to frequency data (Latham *et al.* 2012). Overall, we found that the performance of all occurrence indices was similar, and while their power to detect small effect sizes was low, medium-large effect sizes were detected with high power for several species.

For some species, pellet occurrence indices resulted in greater power than the camera occurrence index, and an equivalent investment in equipment and labour may provide a similar level of power to that achieved using a camera frequency index. Further, our results showed that a large number of plots are generally required to detect medium to large effect sizes using pellet frequency indices, challenging the common preference for collecting pellet frequency data. If simple occurrence metrics can detect meaningful effect sizes, they are likely to be more cost-effective than time-consuming counts (Latham *et al.* 2012). FSC counts are particularly cost-effective, as they do not require plot clearance, although they did not perform well for some species (e.g. a large number of plots were required to detect medium-large effect sizes for rabbit). Occurrence data from scat detections may be particularly useful for rare and elusive species (Seidlitz *et al.* 2021).

Some variation in the spatial and temporal trends detected by the different methods was evident, in line with work by Paton *et al.* (2021), suggesting that they measure slightly different aspects of activity and are subject to different biases. Nonetheless, the influence of such factors appears to be smaller than the magnitude of real change and we show that techniques that sample in different ways, at different scales, can provide comparable indices of activity, as has been found during comparisons of other techniques (e.g. camera trapping and track counts; Espartosa *et al.* 2011).

The applicability of our results to other systems and monitoring programs will depend on objectives and resourcing (Garden *et al.* 2007) and factors that influence the suitability, efficiency and power of monitoring using pellet counts and camera trapping, including species characteristics and population densities, survey timing, habitat type and climate (Towerton *et al.* 2011; Perry and Robertson 2012; Perkins *et al.* 2013). The experimental design, logistics and procedures involved in pellet counts and camera trapping were simple, so either could be implemented without sophisticated training, however, the ability of observers to accurately identify pellets versus images will depend on the target species. If supplementary data, such as animal behaviour observations are required, camera trapping is recommended (Silveira *et al.* 2003; Paull *et al.* 2012), but in areas of high human visitation, pellet counts may be necessary due to the risk of camera theft (Espartosa *et al.* 2011). Occurrence indices may not be suitable where a

species is abundant and ubiquitous due to 'oversaturation' (i.e. not enough absences) (Bengsen *et al.* 2014), in situations where abundance or activity are reduced without causing local extinctions (Bengsen *et al.* 2014), or when a species is rare (Fithian *et al.* 2015). On the other hand, precision of frequency indices from the FAR method is improved when levels of pellet accumulation are high (Campbell *et al.* 2004; Smart *et al.* 2004) and counts from cameras may successfully index visitation at sites where pellet counts are too low to be useful (Kuijper *et al.* 2009). Further, methods can be adjusted according to local conditions to improve the utility of the data. For example, when species are uncommon, camera deployment times (Latham *et al.* 2012) or FAR accumulation times can be increased (Campbell *et al.* 2004; Smart *et al.* 2004) to improve precision and statistical power, without additional costs.

We demonstrated that an activity index derived from camera frequency data was the most powerful wildlife monitoring method for detecting species' responses to management, providing the only index capable of detecting small effect sizes with high power. Our study was restricted to five species at a single location, yet their activity patterns, behaviour, body size and densities varied, and habitat structure varied across the four management treatments examined. Therefore, we believe our results have broader applicability, and advocate camera trapping as a powerful method that can be applied to simultaneously monitor multiple species to improve management outcomes. However, in monitoring programs where funding for cameras is inadequate, but labour resources are readily available, and detection of medium to large effect sizes is adequate to meet objectives, indices derived from pellet count occurrence data should be considered. Occurrence indices derived from FSC and FAR outperformed pellet-based frequency indices in most instances, showing that simple metrics have the potential to detect ecologically important change and improve the cost-effectiveness of monitoring. Nonetheless, with the rapid evolution of camera trapping technology, the efficiency of camera-based methods is likely to increase further as equipment costs are reduced and advances in automated image recognition and processing software are made.

Supplementary material

Supplementary material is available online.

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