

Overcoming the challenges of measuring the abundance of a cryptic macropod: is a qualitative approach good enough?

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Abstract

Context. An understanding of population size and status is necessary for the implementation of appropriate conservation measures to recover threatened taxa. Mark–recapture studies at large spatial scales are impractical and expensive and a rapid survey technique is an attractive option to provide a measure of relative abundance for cryptic species, using indicators of activity.

Aims. The aim of our study was to use conventional methods for population estimation to calibrate a rapid survey technique for the quokka (*Setonix brachyurus*) in the southern forests of Western Australia, with a view to providing quantitative outcomes from this widely adopted monitoring approach.

Methods. We evaluated the accuracy of relative abundances obtained from the rapid survey technique by comparing them with abundance estimates obtained through established methods for the estimation of populations, including web-based mark–recapture and transect-based counts of activity indicators and sightings.

Key results. The rapid survey technique was effective at determining presence of quokkas but resulted in an over-estimation of population size because of inaccurate assumptions about occupancy and relative abundance of animals. An alternative survey method based on counts of fresh faecal-pellet groups was found to provide a more reliable and practical estimation of population abundance ($R^2 = 0.97$).

Conclusions. Activity indices can be used to quantify population abundance, but only for indicators of activity that can be detected readily and for which freshness of activity can be determined.

Implications. Our findings suggest that a rapid survey based on activity indices can be used to evaluate quantitatively the population size of a species that is rare and potentially mobile at a landscape scale. The attraction of these techniques is that they provide a rapid and inexpensive survey option that is potentially applicable to any cryptic and/or threatened species and is practical for resource-constrained land managers.

Additional keywords: faecal pellets, indirect survey method, population size estimates, quokka, rapid survey, relative abundance, runnels, *Setonix brachyurus*, sightings, tracks.

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Introduction

The ability to measure population size is critical for making informed management decisions, particularly for threatened species. However, in some cases it is difficult to obtain accurate estimates of abundance because of the investment of time and resources required for intensive mark–recapture studies and the assumptions of many statistical models that require high detection probabilities and large numbers of animals (Caughley 1977; Gardner and Mangel 1996; Bolen and Robinson 1999; Anderson 2001; Defos du Rau *et al.* 2003). These challenges are acute for cryptic and/or threatened species that often occur at low densities, display secretive behaviour, and/or occupy relatively inaccessible habitat (Conroy 1996; McKelvey and

Pearson 2001; Hamm *et al.* 2002). Indirect methods of surveying population size are often considered a more cost effective and practical alternative to mark–recapture studies, despite weaknesses documented in the literature relating to known biases, inconsistent detection and an inability to meet model assumptions (Nichols and Pollock 1983; Montgomery 1987; Slade and Blair 2000; McKelvey and Pearson 2001; Hopkins and Kennedy 2004). Indirect monitoring techniques such as the use of photographic captures (Karanth and Nichols 1998), driving transects (Caro 1999; Olson *et al.* 2005), walked line transects (Short and Turner 1991; le Mar *et al.* 2001; Poole *et al.* 2003; Wayne *et al.* 2005) and dung-pellet counts (Johnson and Jarman 1987; Allen *et al.* 1996; Buckland *et al.* 2001;

Hayward *et al.* 2003) have been widely used to provide a quantitative estimate of population size for small and medium-sized mammals. More recently, these have been coupled with sophisticated models that can actively account for changing detection probabilities (e.g. Anderson 2001; Buckland *et al.* 2001; Bailey *et al.* 2004, 2007). The result is more accurate estimates, but often a requirement for a large sample size, which remains challenging for cryptic species and impractical for field application by land managers and practitioners involved in rapid and responsive decision making for the management of threatened species.

The quokka (*Setonix brachyurus*) is a wallaby listed as vulnerable (IUCN 2013). It is restricted to south-western Australia and two near-shore islands, Rottnest and Bald Island (White 1952; Storr 1964; Maxwell *et al.* 1996; Sinclair 1998). On the south-western Australian mainland, quokkas occur in three areas, namely, the northern jarrah (*Eucalyptus marginata*) forest between Preston River and Perth, disjunct reserves around Albany, and the continuous southern forest between Collie and Denmark (Sinclair 1998; de Tores *et al.* 2008).

There is a greater level of habitat connectivity within the southern forest and preliminary DNA analysis suggests that animals are more likely to move among habitat patches in a functioning meta-population (P. Spencer, unpubl. data). If this is the case, then the southern forest population of quokkas is likely to be important in terms of genetic diversity and resilience to disturbances and demographic fluctuations. Currently, little is known about the ecology or conservation status of quokkas in the southern forests of Western Australia. A cost-effective but reliable and practical technique for determining population size is fundamental to understanding the ecology of the quokka in this area and for the implementation of effective conservation and management actions.

Capture-mark-release methods can provide reliable population abundance estimates, particularly when detection probability is accounted for through population modelling. This technique is time consuming, inefficient and expensive for quokkas in the southern forest because of the large area of potential habitat, much of which is remote and inaccessible, dense vegetation, where quokkas move using intricate runway tunnels (called 'runnels') and the seasonal movement patterns of quokkas, which make their direct observation, detection and capture more challenging, particularly in the southern part of their range (K. Bain, unpubl. data). In the northern jarrah forest, transect counts of faecal-pellet groups have been used to estimate population densities of quokkas in discrete swampy habitat (Hayward *et al.* 2005). This approach is potentially applicable to the southern forest population, but is likely to be more challenging because of the higher density of vegetation and the movement of quokkas across the landscape.

In 2003, a rapid survey technique was devised to provide a qualitative measure of relative abundance (i.e. high, medium, low) using the subjective assessment of indicators of activity including faecal pellets, runnels, tracks and sightings (G. Liddelow, pers. comm.). The technique (hereafter called the 'Liddelow rapid-survey technique') has been widely adopted by land managers throughout the south-west of Western Australia, but the relative abundance categories have not been validated and cannot provide a quantitative estimate

of population size. In the present study, we tested the hypothesis that indices of activity such as faecal pellets, runnels, tracks and sightings can be used in a rapid-survey approach to quantify the abundance of quokkas in the southern forests of Western Australia. We used established field techniques for the estimation of populations to evaluate the subjective categorisation of quokka abundance through the Liddelow rapid-survey technique, with a view to providing quantitative outcomes from this widely adopted monitoring approach.

Materials and methods

Study sites

The southern forests occur between Collie and Denmark in the far south-west of Western Australia and encompass the Southern Jarrah and Warren biogeographical subregions (IBRA 2004). This study was undertaken in a subset of these forests between Manjimup and Walpole. About 85% of the 10 000-km² region is primary native vegetation that is publicly vested and managed by the Department of Parks and Wildlife (DPAW). The human population in the area is low (<8000) and concentrated in and around four town centres. The region has a Mediterranean-type climate, with warm dry summers and mild wet winters. Between 2001 and 2011, the average annual rainfall in the southern part of the region was 1098 mm, of which only 12% fell in the four driest months (December–March; Bureau of Meteorology 2012). The vegetation consists of a mosaic of forest, woodland, shrub land, wetland and coastal ecotypes, often with complex vegetation structure and dense understorey. The tall forests in which this study was conducted are dominated by jarrah, karri (*Eucalyptus diversicolor*), marri (*Corymbia calophylla*) and tingle (*Eucalyptus jacksonii*, *E. guilfoylei* and *E. brevistylis*). The native forest is largely contiguous, with large areas inaccessible by road, such as the Walpole Wilderness area (325 116 ha). The dense understorey makes the forest effectively impenetrable to humans in most places.

In total, 137 habitats between Manjimup and Walpole were surveyed for quokkas by using the Liddelow rapid-survey technique. The technique consisted of field observations of the apparent level of quokka activity, as evidenced by runnels, faecal pellets, tracks and incidental sightings. Surveys targeted defined habitat most likely to be occupied by quokkas, such as creek lines and swamps. Searches for quokka activity continued until the observer was satisfied that they had obtained an adequate assessment of the site, typically in less than 30 min. Where quokka activity was recorded, the observations of runnels, faecal pellets, tracks and incidental sightings were then integrated to derive a qualitative and relative estimate of quokka abundance, which was rated subjectively as low, medium or high.

A subset of 12 study sites was then selected on the basis of relative-abundance categories obtained through the Liddelow rapid-survey technique, including four sites each for low, medium and high abundance (Fig. 1). At each site, a trapping web was established, with a central axis following a creek line. Eight lines radiating from the centre were each 240 m long. Population abundance estimates obtained through mark-recapture were used as an indicator of true abundance

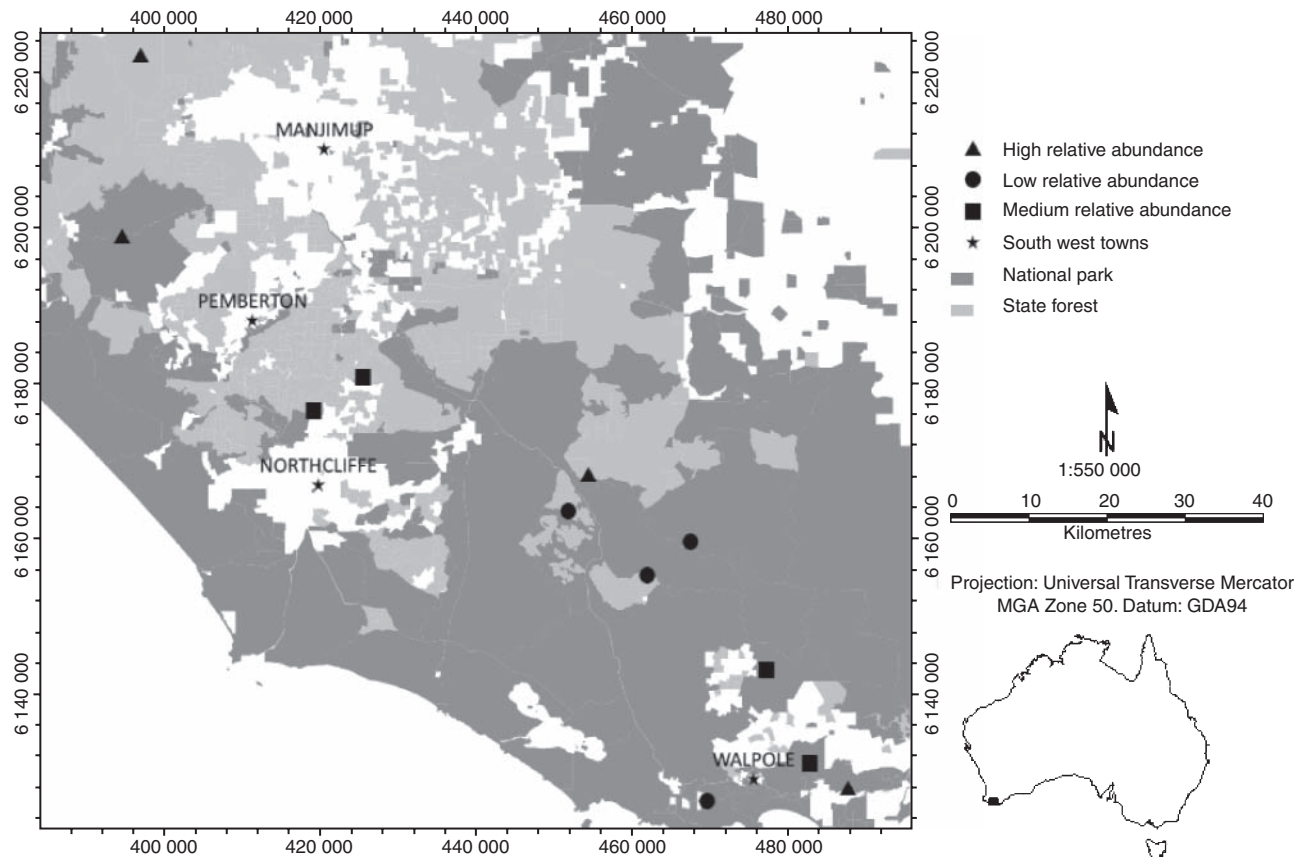


Fig. 1. The 12 study sites representing four sites each at low, medium and high abundance of quokkas (*Setonix brachyurus*) according to the Liddellow rapid-survey technique.

and were compared with the relative abundances given to each of the 12 sites by application of the Liddellow rapid-survey technique.

The components of the Liddellow rapid-survey technique (runnel counts, faecal-pellet counts, track counts and incidental sightings) were then compared individually to the population abundance estimates obtained through mark–recapture. Each of the methods is described in detail below.

Mark–recapture

Quokkas in the northern jarrah forest are considered trap shy (Hayward *et al.* 2003) and it was expected that the same would apply in the southern forests. Southern populations are also likely to move between suitable habitat patches and abundance estimates may be confounded by immigration and dispersal, particularly at extremely low densities and with sparse data. For the purpose of the present study, the trapping regime was completed within one optimal time period to minimise the effect of temporal variation and the potential effect of replacement owing to the movement of animals between the populations. Autumn was selected as the optimal period for trapping because of the moderate weather conditions and early sunrise, which reduce exposure and stress to captured animals. The choice of autumn was also considered to be likely to maximise detection

probability, because the core habitat is drier, potential food resources are more restricted, quokkas are concentrated near well defined creek lines and have a much smaller and stable home range (K. Bain, unpubl. data).

Trapping webs were selected instead of trapping grids, to provide the capacity to relate population estimates to the area of habitat the quokkas occupied (Anderson *et al.* 1983; Buckland *et al.* 1993). These were established following the recommendation of Anderson *et al.* (1983) that trap spacing should result in at least 8–12 traps per home range in the centre of the web. Because there are no reports on the home range of the quokka in the southern forest, the spacing along each line was determined using the home range of 6 ha for quokkas in the northern jarrah forest (Hayward *et al.* 2004). This resulted in an average density of 14.1 traps ha⁻¹ in the centre of the web. Each web consisted of 65 traps 30 m apart and trapped an effective area of 18.1 ha. After a 3-day pre-feeding period, trapping was conducted for 10 consecutive nights by using ‘Thomas’ soft-wall traps, made with shade cloth stretched over a steel frame (450 × 450 × 800 mm, Sheffield Wire Works, Welshpool, Western Australia) and baited with apples. The main non-target species in this area was *Rattus fuscipes*. For this reason, the Thomas traps were modified to include a reinforced rat-sized escape hole in the back of the trap and the trigger plate was adjusted so that rats would not set off the

trap. Captured quokkas were removed from traps, weighed, ear-tagged with unique identity codes and released. Pes measurements, pouch condition and presence of pouch young were also recorded. The establishment of trapping webs, trap set and trap checking took an average of 87 man hours per site, factoring in the density of the vegetation, the intricacies of web establishment, the labour associated with getting traps onsite, pre-feeding and the need for two people to check the traps to ensure they were cleared within 3 h after sunrise, as per standard operating procedures of the DPaW.

Sign and sighting surveys

Runnel counts, track counts and faecal-pellet counts were undertaken at each site 10 days before trapping, to ensure that counts were not influenced by the presence of traps or bait (Wayne *et al.* 2005). Eight transects, each 240 m long, were established as a part of the trapping web and were visited each morning for 10 consecutive days. Use of the web arms as the focus for all measurements was necessary because of the density of the habitat, the damage that constructing additional transects would have caused to the runnel network and the possibility of creating access for feral predators through the habitat. Each of the rapid-survey elements when applied at a transect level took an average of 3 h per site. Trapping web arms were used as transects, and so, additional time would need to be allowed if these rapid survey elements were applied in isolation. Transect establishment could be undertaken in conjunction with the counts, and a much lower standard of transect, and a lower associated level of disturbance to the vegetation, would be needed. Transect establishment and counts would be expected to take approximately 8 h per site.

Fresh faecal-pellet groups identified by their soft exterior and green colour when broken apart (Hayward *et al.* 2003) were counted and collected daily to avoid repeat counting on subsequent days along each transect. All fresh pellets were also removed on the day before counts commenced, to ensure that only fresh pellets were counted on the first day of survey. The clearance of pellets also circumvented the need to estimate faecal-pellet disappearance rates (Buckland *et al.* 2001), which varies significantly in different habitats and under different weather conditions (K. Bain, pers. obs.).

Track counts were completed by clearing a small area of leaf litter at the entrance or within selected runnels, to expose the sandy substrate underneath. The clearings were visited each morning and those with quokka tracks present were recorded and the surface smoothed free of tracks. There was no attempt to determine whether more than one animal had moved across a single pad. Runnel counts were completed by counting active runnels, identified by compacted leaf litter and an absence of fallen debris, crossing each transect. When animals were physically observed during surveys, these were recorded as sightings.

Analysis of data

Population abundance estimates using mark-recapture

Program distance (Thomas *et al.* 2010) was considered for generation of density estimates from the capture records. However, the assumption that all animals near the centre of

the web are captured with certainty (Buckland *et al.* 2001) could not be met, as evidenced by remote cameras.

Population size was calculated from capture records within the trapping period, using MARK closed capture models with heterogeneity (White and Burnham 1999). The use of Jolly-Seber models was considered, because these are open population models allowing for immigration, emigration, recruitment and mortality during the trapping period (Lefebvre *et al.* 1982). However, these models assume that capture probabilities vary only by trapping occasion and do not allow for heterogeneity or behavioural response to trapping, and, in our study, individual heterogeneity was considered to be an important potential source of bias for capture probabilities. Mark-recapture was conducted for a short time period within habitats that are geographically defined because of topography and/or landform and the fact that quokkas do not move out of the creek systems during the selected survey period (K. Bain, unpubl. data). It was, therefore, considered that the data met the closure criteria to enable the use of closed capture models with heterogeneity (Lefebvre *et al.* 1982; Kendall 1999).

The effective sampling area was consistent across webs and we have included this area in the methods to enable the reader to convert the abundance to a density if they prefer; however, abundance values are used throughout this article for ease of communication.

Model selection was based on the Akaike information criterion (Akaike 1973) corrected for small sample size (AICc). AICc was interpreted as a measure of the lack of fit from the 'true' model and the model with the lowest AICc value was considered the most appropriate (Burnham and Anderson 1998). The models included the effect of factors such as trap response, time, group behaviour and individual heterogeneity on the probability of capture and recapture (Table 1).

Testing the Liddelaw rapid-survey technique

The population abundance estimates obtained through MARK were compared with those from the Liddelaw rapid-survey technique by using ANOVA, with population abundance as the response variable and relative abundance category as the group (Stata10, StataCorp. 2007). Bonferroni multiple-comparison tests were used to compare the population abundance estimates by relative abundance to account for the detected variance among groups.

Testing individual components of the Liddelaw rapid-survey technique

At each site, the numbers of runnels, tracks, faecal-pellet groups and sightings of quokkas were each divided by the number of visits to obtain average counts of runnels, tracks, faecal pellets and sightings for each site to use as independent variables in linear regressions. These values were used in a linear regression (Stata10, StataCorp. 2007) that modelled all possible combinations of runnels, faecal pellets, tracks and sightings against population abundance estimates obtained in MARK. Model selection was based on the AICc and the model with the lowest AIC value was considered the best fit (Burnham *et al.* 1995). R^2 -values were used to determine

the level of model uncertainty and the potential need for model averaging.

Distance sampling was considered for estimating the abundance of quokkas from each of the activity indices, but the replication required for model robustness and some of the model assumptions, particularly those relating to randomly placed lines or points, could not be met within the sensitive habitats being surveyed (Buckland *et al.* 2001).

Results

Population abundance estimates using mark-recapture data

Estimates of population size (\hat{N}) for each of the 12 sites were obtained using a family of models generated in program MARK (White and Burnham 1999) that incorporated several sources of variability in the probability of capture. AICc weights were computed for all candidate models (Table 2). Temporal and behavioural heterogeneity, as well as individual heterogeneity, contributed to capture success, as suggested by the AICc weights (Table 2); however, the contribution was slight, as indicated by the relatively high capture probabilities generated for all models.

The capture probability was high enough to justify the use of the derived population estimate from the MARK modelling (hereafter referred to as 'population abundance') as a measure of the actual population size, given that even the weakest model produced a capture probability of 1.0 by Day 4 of the 10-day trapping period.

Testing the Liddelow rapid-survey technique

There was a strong relationship between the relative abundance categories and the mean population abundance estimates calculated for each site (Fig. 2). The population abundances for sites categorised as low or medium were significantly different ($P=0.025$), with 1.25 and 4.75 individuals, respectively. There was also a significant ($P=0.037$) difference in the mean population abundance between sites with a medium and those with a high relative abundance, with 4.75 and 8.5 individuals, respectively. The range of values, however, was not discrete in sites categorised with medium and high abundance, showing that as the abundance of animals increases, the categorisation of relative abundance becomes more difficult (Fig. 2, Table 3).

Table 1. Combination of factors modelled using Program MARK (Gary C. White, Department of Fishery and Wildlife, Colorado State University)

Model name	Model description
Huggins closed population estimation	
Mo $p(.) = c(.)$, N	Probability of capture and recapture constant
Mo2 $p(.) = c(.)$, N	Presence of capture influence on recapture
Mt $p(t) = p(t)$, N	Presence of an equal temporal effect on capture and recapture
Mt2 $p(t) = c(t)$, N	Presence of temporal effect on capture and recapture
Mt3 $p(t) = c(t)$, N	Presence of a temporal effect on capture only
Mg $p(g) = c(g)$, N	Presence of a site effect on capture and recapture
Mb $p(.) = c(.) + \text{constant } (b)$, N	Presence of behavioural influence (e.g. gender) on capture and recapture
Mtb $p(t) = c(t) + \text{constant } (b)$, N	Presence of temporal and behavioural influence on capture
Closed captures with heterogeneity	
Mh $pa(.) = pb(.)$, N	Presence of individual heterogeneity in capture
Mbh $pa(.) = pb(.)$ beh constant N	Presence of behavioural and individual heterogeneities in capture

Table 2. Combinations of factors modelled with Program MARK Closed Captures with heterogeneity, their Akaike information criterion corrected for small sample size (AICc) weights and derived capture probabilities

Model name	AICc weight	No. of parameters	Mean daily capture probability	Standard error
Huggins closed population estimation				
Mtb $p(t) = c(t) + \text{constant } b$	0.48346	7	0.5142857	0.3379835
Mt3 $p(t) = c(t)$	0.17080	2	0.5760092	0.0327577
Mo2 $p(.) = c(.)$	0.10304	2	0.3514978	0.0558929
Mb $p(.) = c(.) + \text{constant}$	0.10304	2	0.3514977	0.0558929
Mo $p(.) = c(.)$	0.09964	1	0.4189930	0.0274523
Mt $p(t) = c(t)$	0.03824	7	0.4415591	0.0694546
Mt2 $p(t) = c(t)$	0.00173	12	0.5879423	37.0610435
Mg $p(g) = c(g)$	0.00004	24	0.4419041	0.1490455
Closed captures with heterogeneity				
Mh $pa(.) = pb(.)$	1.0000	1	0.7285714	0.0130957
Mbh $pa(.) = pb(.)$ beh constant	1.0000	1	0.7130252	6.02619914

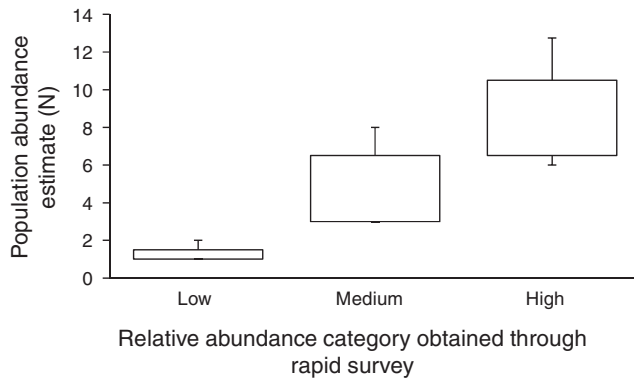


Fig. 2. Variance in the actual abundance (mark–recapture) for sites categorised as having a relative abundance of low (mean=1.25 individuals), medium (mean=4.75 individuals) and high (mean=8.5 individuals). The mean population abundance is significantly different between the sites categorised as having a relative abundance of low or medium ($P=0.025$) and those having a relative abundance of medium and high ($P=0.037$).

Table 3. Population abundance estimates, faecal-pellet counts, runnel counts, track counts and sightings for sites categorised as having a relative abundance of low, medium and high through the Liddelow rapid-survey technique

Study site	Relative abundance category	Population abundance estimate (\bar{N})	Faecal-pellet count	Runnel count	Track count	Sighting count
1	Low	1.0	1.1	12.0	0.0	0.0
2	Low	1.0	1.1	18.0	0.0	0.0
3	Low	1.0	1.3	9.0	0.1	0.0
4	Low	2.0	1.3	22.0	0.0	0.0
5	Medium	3.0	2.6	27.0	0.0	0.0
6	Medium	3.0	2.7	18.0	0.0	0.0
7	Medium	5.0	4.4	16.0	0.0	0.3
8	Medium	8.0	5.1	31.0	0.2	0.2
9	High	6.0	5.8	28.0	0.0	0.0
10	High	7.0	7.3	66.0	0.1	0.2
11	High	8.0	8.3	21.0	0.1	1.6
12	High	13.0	12.5	76.0	0.0	0.3

Testing individual components of the Liddelow rapid-survey technique

The strongest model for predicting population abundance was based solely on faecal-pellet counts and a strong linear relationship was demonstrated between faecal-pellet counts and population abundance ($R^2=0.966$, AIC 24.04, Table 4, Fig. 3). The models containing pellet counts combined with other estimate techniques were also strong. There was a minimal change in the AICc values at the removal of track counts and sightings from the model, and where these were the only elements in the model, they demonstrated poor correlation with population abundance ($R^2=0.18$ and 0.025 , respectively) and had high AICc values, which suggests that they were not contributing to model strength.

There was a sound linear relationship between runnel counts and population abundance ($R^2=0.697$), but the data seemed

Table 4. Modelled activity indices for the prediction of quokka abundance (N) in the southern forest

AICc, Akaike information criterion corrected for small sample size

Model (N , dependent variable)	R^2	AICc	Delta AICc
N , pellets	0.966	24.041	0.000
N , pellets, runnels, tracks, sightings	0.976	25.698	1.657
N , pellets, runnels	0.967	25.701	1.660
N , pellets, runnels, tracks	0.967	27.448	3.660
N , runnels, sightings	0.732	45.198	21.157
N , runnels, tracks, sightings	0.736	48.875	24.834
N , runnels	0.697	50.303	26.262
N , runnels, tracks	0.702	52.137	28.096
N , sightings	0.183	62.241	38.200
N , tracks	0.025	64.353	40.312
N , tracks, sightings	0.183	65.236	41.195

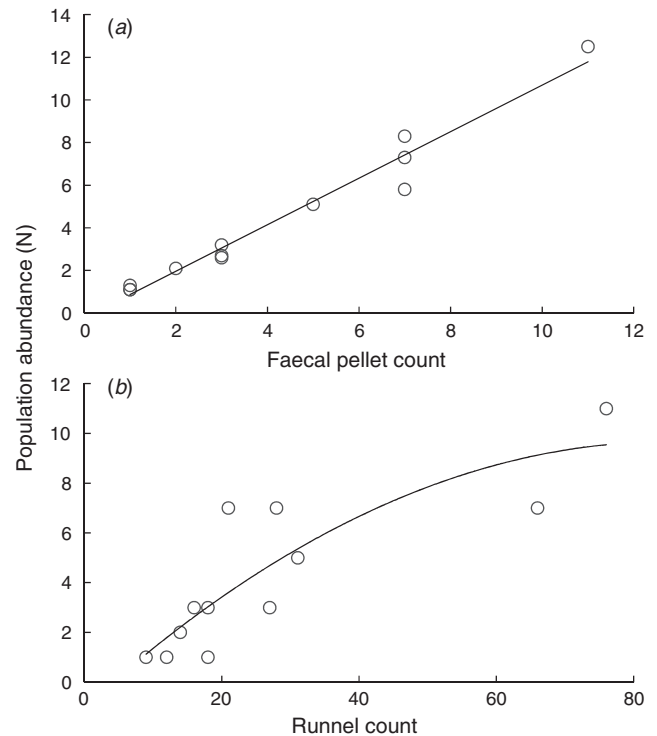


Fig. 3. (a) Linear relationship between faecal-pellet counts and population abundance (N) and (b) quadratic relationship between runnel counts and population abundance (N).

more inclined toward a quadratic relationship (Table 4, Fig. 3) and the high AICc values for models containing runnel counts without pellet counts showed that these are weak models for predicting population abundance.

Defining a quantitative survey technique

The linear relationship between faecal-pellet counts and population abundance estimates (N) can be represented by the equation $N=1.09(x) - 0.21$, where x =number of faecal pellet groups and N =estimated population size.

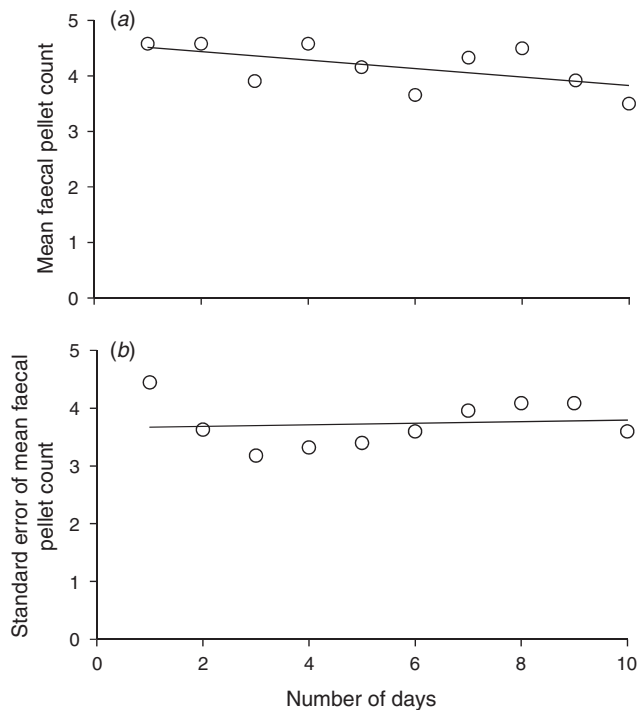


Fig. 4. (a) Mean number of faecal pellets and (b) the standard error recorded for all sites over the 10-day survey period.

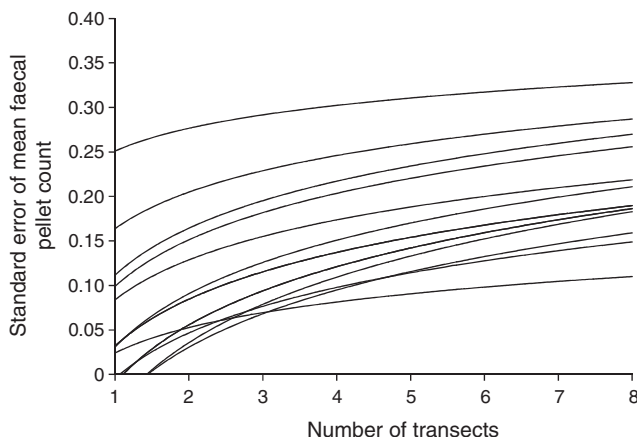


Fig. 5. Logarithmic trend lines for the standard error of mean faecal-pellet counts across eight transects at each of the 12 study sites.

The mean number of faecal-pellet groups and the standard error were calculated across all sites for each day when the counts were undertaken (Fig. 4). The point at which the standard error stabilised determined the adequate sample regime for estimating abundance from pellet counts, with minimal variation around the calculated mean. The standard error was stable from the first day of survey, suggesting that a single visit to each site is adequate; however, all fresh-looking pellets were removed before counts commenced, to ensure that fresh pellets were from the previous night.

Similarly, the mean number of faecal-pellet groups and the standard error were calculated at a site level for each length of

transect where counts were undertaken (Fig. 5). The point at which the standard error stabilised determined the minimum number and length of transects required for an optimal sample regime. For three of the sites, the standard error of the mean was stable following collection of samples from a single transect (240 m); for two sites, the standard error was stable after two transects (480 m); for one site, the standard error was stable after three transects (720 m) and, for six sites, the standard error of the mean was stable following collection of samples from four transects (960 m).

Discussion

The present paper makes an important contribution to the problem of surveying cryptic and rare mammals, and is a timely contribution, given that the Liddelow rapid-survey technique is being widely implemented in quokka surveys in the southern forest. We found that faecal-pellet counts alone performed better than the composite Liddelow rapid-survey technique because runnels, tracks and sightings generated unreliable estimates and confounded the overall estimate of abundance. Faecal-pellet counts correlated very strongly with the population abundance of quokkas, demonstrating that the Liddelow rapid-survey technique can be refined back to a quantitative method based on faecal-pellet counts that is simple, rapid and accurate.

To obtain a reliable rapid estimate of population abundance, a minimum of 960 m of transect should be surveyed on two repeat visits, including the first visit to establish pre-existing pellets and the second to count new pellets. Variation in detection probability should be considered by undertaking surveys at the same time of the year with the same amount of moisture in the landscape (e.g. late summer and early autumn before the opening autumn rains when quokkas are concentrated in the moister parts of the landscape and food is limited), at the same time of the day (e.g. morning, when fresh faecal pellets are easier to detect due to their moist exterior) and using observers that are trained to identify fresh faecal pellets and differentiate the faecal pellets of quokka from those of western brush wallaby (*Macropus irma*).

Discriminating fresh from older pellets is critical for using this method to estimate quokka abundance. At all sites, faecal pellets were consistently deposited in the proximity of previously recorded faecal-pellet deposits, despite these pellets having been removed. Capture patterns on the trapping webs showed that sections of the web were routinely visited by the same group of quokkas. Determining the age of quokka faecal pellets is challenging because of the high variability of the rates of decay of pellets over space and time (K. Bain, pers. obs.). Failure to do so can substantially overestimate population abundance owing to persistence of old pellets, the accumulation of pellets in areas routinely visited by the same group of animals, and variation in the temporal and spatial use of habitat by quokkas. Although daily removal of faecal pellets can overcome this bias, it may also reduce the deposition rate in subsequent days if animals share common latrine areas or are motivated to defecate where they encounter old pellets (Vernes 1999). Differentiating faecal pellets produced by quokkas from those produced by the western brush wallaby is also a potential

source of error (Triggs 1996; Hayward *et al.* 2005). Some moderate level of observer skill is therefore necessary to ensure that quality data are collected.

There was a significant linear relationship between runnels and population abundance, but the data appeared more inclined toward a non-linear relationship, such as a quadratic relationship. This might be expected because quokkas use and share runnels to move through their habitat, creating an access network through suitable habitat. At low animal densities, an approximate linear relationship in the number of runnels would be expected. However, at higher densities it is logical that the number of runnels within the network would plateau as access to all suitable habitat is achieved. Incidentally, whereas the number of runnels may plateau at increasingly higher quokka densities, the average frequency of use of runnels would be expected to continue to increase. To verify this, more data would need to be collected at the sites of highest density. Although runnels are the most conspicuous sign of quokka activity, determining currency of use is more difficult because of their temporal persistence and their use by other animals. In dense vegetation, runnels create an access network through and between suitable habitat, which is used by quokkas as well as other species including southern brown bandicoots (*Isodon obesulus fusciventer*) and common brush tail possums (*Trichosurus vulpecula hypoleucus*). Therefore, runnels may be useful for determining that the habitat has been occupied by quokkas, but they are less effective as a means for determining abundance or recentness of activity.

The use of tracks and sightings were unreliable because individuals and their tracks were undetectable at most sites because of dense vegetation, a lack of exposed and suitable substrate, the wind causing movement of vegetation that swept the sand of tracks and the presence of other animals. The use of baited or unbaited sand pads described by Mawson and Orell (2001) to assist with track detection may help overcome substrate limitations; however, practical considerations such as sand free from the introduced plant pathogen, *Phytophthora cinnamomi*, would need to be addressed; a certified disease-free sand supply was not available for the present study.

Remote cameras were unavailable in sufficient numbers to be used for population-size estimates in the present study, but are likely to be an efficient and useful quantitative technique for monitoring in remote and difficult terrain, with minimal resources and minimal environmental disturbance (Rowcliffe *et al.* 2008). Cameras are likely to provide more reliable and accurate activity indices than faecal-pellet counts and other indirect measures, particularly in poor weather conditions (Glen and Dickman 2003; Thomas *et al.* 2010; Hamilton and Rolfe 2011).

Indirect methods such as faecal-pellet counts and camera trapping rates can be practical and reliable techniques for estimating population abundance. The attraction of these techniques is that they provide a rapid and inexpensive survey option that is potentially applicable to any cryptic and/or threatened species and is practical for resource-constrained land managers. Although these may be rapid approaches to monitoring, there are several factors that are likely to affect detection probability among years, areas or observers and an understanding of how this variation can be accounted for is

important, such as through a combination of systematic or stratified sampling, tightening up standard monitoring protocols, measuring key covariates, and/or estimation of detection probability using mark-recapture, distance or occupancy models, where this is achievable and practical.

Quokkas have morphological features such as face dimensions, ear damage, body condition, body size and shape that could be used to differentiate individuals on camera traps, within a short period of time. Therefore, capture-recapture models to estimate abundance, based on the re-trapping of recognisable individuals by cameras, may be possible for this species. Models of occupancy (MacKenzie *et al.* 2002) that can estimate underlying detection probabilities from faecal-pellet counts or camera trapping data could also be adopted, if the assumptions of the models can be met and where the proportion of area used by the species can be used to evaluate population trends reliably. Given the ready detectability of quokkas from faecal pellets and runnels, occupancy modelling has the potential to become a valuable tool for monitoring quokka population trends in the southern forest.

In the interim, the present study has provided a robust and defensible test of the Liddelow rapid-survey technique, showing that it can be paired back to a quantitative method based on faecal-pellet counts. The method is useful because of its simplicity and ability to be applied over large spatial scales in a relatively short period of time. Although the faecal-pellet method is not as rapid as the Liddelow approach, it still takes less than 10% of the time that trap-based mark-recapture surveys would take for this species. With a focus on standard monitoring protocols, this technique could be rolled out across the southern forest, with minimal variation in observer bias, as opposed to the widely used Liddelow rapid-survey technique, which is purely subjective. If this was to be undertaken, it could generate the first accurate estimate of abundance for quokkas in the southern forests and significantly improve the capacity of land managers to make important conservation decisions for the management of this unique species in this challenging landscape.

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