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Precision, accuracy and bias of walked line-transect distance sampling to estimate eastern grey kangaroo population size

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Abstract

Context. Distance sampling is widely used to estimate the size of wildlife populations, including kangaroos. However, the performance of distance-sampling abundance estimates has seldom been evaluated for wild mammal populations of known size.

Aims. We evaluated the precision, accuracy, bias and interval coverage of abundance estimates from walked line-transect sampling, a commonly used distance-sampling method, for a marked free-ranging population of eastern grey kangaroos (*Macropus giganteus*) at Yanakie Isthmus, Wilsons Promontory National Park, south-eastern Australia.

Methods. In each of two study periods (November 2012 and May 2013) we first determined the true size of the uniquely marked kangaroo population by conducting 10 intensive searches of the study area. We then conducted distance sampling along six systematically spaced line transects. We walked each transect four times in November 2012 and seven times in May 2013. Data were analysed using Program DISTANCE.

Key results. Our intensive searches revealed that 141 and 124 collared kangaroos were present in the study area in November 2012 and May 2013, respectively. When transects were walked four or more times (i.e. ≥400 observations), maximum precision (coefficient of variation; CV of ~13%) was achieved in both survey periods. Walking transects twice (i.e. ~200 observations) produced abundance estimates with CVs of <20% in each study period. The accuracy (root mean square error) of abundance estimates varied from 1 to 13 (November 2012) and from 3 to 28 (May 2013). Bias ranged from −9% to +23%, but stabilised at between −1% and −9% when transects were walked four or more times in each study period. The 95% confidence intervals for the abundance estimates always included the true population size.

Conclusions. Our results indicated that walked line-transect distance sampling is a precise and accurate method for estimating eastern grey kangaroo abundance. The small negative biases that occurred when sample sizes were large were likely to be due to some animals moving outside the study area.

Implications. Provided that the key design elements and assumptions are met, estimates of kangaroo abundance from walked line-transect distance sampling should have good precision (CV < 20%) and minimal (<10%) bias.

Additional keywords: abundance estimation, Australia, coefficient of variation, density estimation, interval coverage, macropods, *Macropus giganteus*, marked individuals, multiple-covariate distance sampling, Wilsons Promontory National Park.

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Introduction

Estimating population size or density is fundamental to many aspects of wildlife research and management (Seber 1982; Thompson *et al*. 1998; Williams *et al*. 2002). Methods that reliably provide precise, accurate and unbiased estimates of animal abundance are therefore required. Direct estimates, such as total counts or sample counts, are generally preferable to indirect estimates of abundance (Thompson *et al*. 1998; Anderson 2001; Williams *et al*. 2002).

One technique that has been widely used to directly estimate the abundance of wildlife populations is distance sampling, which is believed to provide robust estimates when its key assumptions are met (reviews in Burnham *et al*. 1980; Seber 1982; Buckland *et al*. 1993, 2001, 2004, 2005; Thomas *et al*.

2010). In the most widely used form of distance sampling, line-transect sampling, the observer moves along linear transects and records the perpendicular distance from the transect line to each object of interest, or cluster of objects, sighted (Buckland *et al.* 1993, 2001, 2004, 2005; Thomas *et al.* 2010). Intuitively, objects closer to the transect line are more likely to be detected (Buckland *et al.* 2005), and the analysis models the detection function, the probability of detecting an animal as a function of its distance from the line (Burnham *et al.* 1980; Buckland *et al.* 1993, 2001, 2004). Objects missed during line-transect surveys are estimated from the detection function, and density is extrapolated from the effective area sampled to estimate abundance for the entire study area (Buckland *et al.* 1993, 2001). Line-transect sampling relies on the following four key assumptions: (1) all animals on the transect line are detected, (2) measurements are unbiased, (3) animals are detected at their initial locations, and (4) the detection function has a 'shoulder' (Buckland *et al.* 1993, 2001). If these assumptions are not met, then the estimates of abundance can be inaccurate and biased. It has been suggested that a distance-sampling abundance estimate within 10% of the true abundance will be useful for many wildlife-management purposes (Anderson and Southwell 1995). The precision (i.e. the standard error of the estimate relative to its mean; Williams *et al.* 2002) of abundance estimates is also important. Precision of distance-sampling estimates depends on the uncertainty in the detection function, changes in the encounter rate between transects, and the size of observed clusters (Buckland *et al.* 2001). As a rule of thumb, it is desirable that the precision of abundance estimates be <20% (Buckland *et al.* 1993, 2001; Skalski *et al.* 2005).

Although line-transect sampling has commonly been used to estimate the abundance and density of wild mammals (e.g. Southwell 1989; Plumptre 2000; Ickes 2001; Focardi *et al.* 2002; Dique *et al.* 2003; Ariefiandy *et al.* 2013), few studies have evaluated the precision and accuracy of line-transect sampling for wild, unenclosed mammal populations of known size (but see Southwell 1994; Hounsome *et al.* 2005). The objective of the present study was to assess the precision, accuracy, bias and interval coverage of estimates of line-transect sampling for a wild, unenclosed population of eastern grey kangaroos (*Macropus giganteus*) in south-eastern Australia. Many kangaroos in this population were individually marked, providing a unique opportunity to robustly compare estimates of abundance from walked line-transect sampling with a population of known size. Coulson and Raines (1985) suggested that the large size (Coulson 2008), conspicuous hopping gait (Dawson 2012) and use of open habitats for feeding (Taylor 1980; Moore *et al.* 2002) make this species ideal for walked line-transect sampling. The method has subsequently been used to estimate the abundance of this species (e.g. Southwell 1984, 1994; Fletcher 2006). Walked line-transect sampling has also been used to estimate the abundance of other macropodids (e.g. Southwell 1989, 1994; Coulson 1993; Southwell *et al.* 1995; Clancy *et al.* 1997; Stirrat 2008).

Materials and methods

Study area

We conducted the study at Yanakie Isthmus airstrip, Wilsons Promontory National Park, Victoria, south-eastern Australia

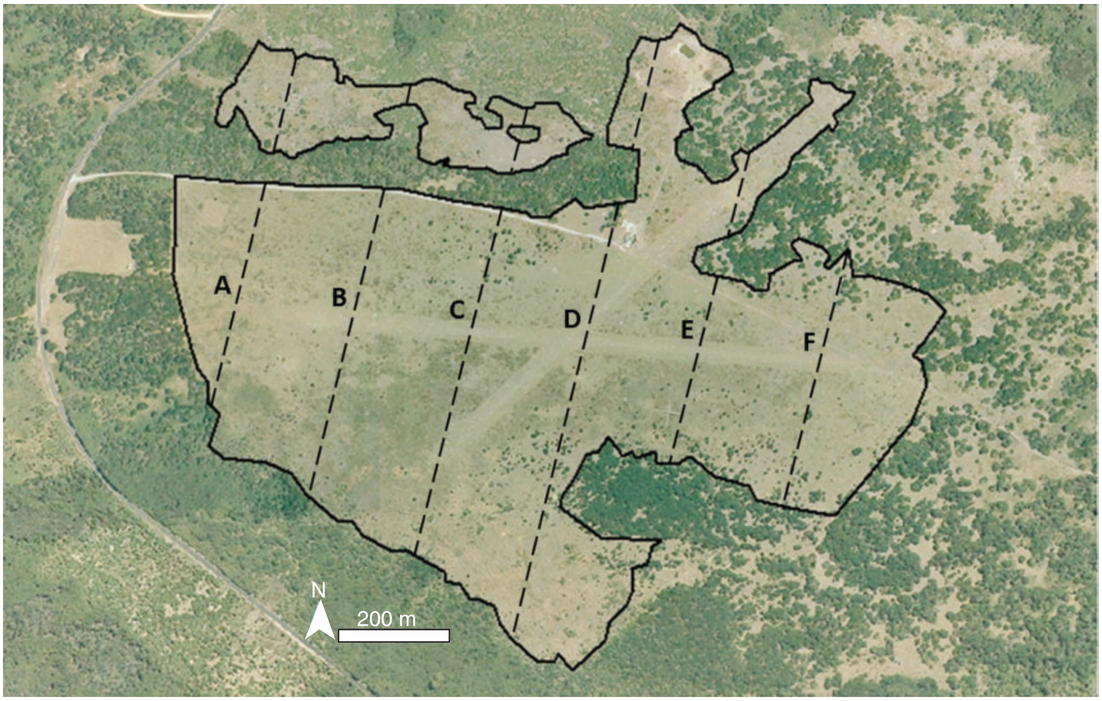

Fig. 1. Aerial photograph of the study area at Yanakie Isthmus airstrip, Wilsons Promontory National Park, south-eastern Australia. The study area boundary (solid black line) and the six walked line transects (dashed black lines labelled A–F) are shown. The two mown runways, and occasional thickets, are also visible within the study area.

(38°56′58″S, 146°17′2″E, 22 m above sea level; Fig. 1). The airstrip has two runways and two helipads, which are mown twice annually (Fig. 1). Centred over the airstrip, the 76-ha study area consisted of two habitats, namely, 'grass' and 'rush' (Fig. S1, available as Supplementary Material on the *Wildlife Research* website). Grass was dominated by coast blown grass (*Lachnagrostis billardieri*), couch grass (*Bromus diandrus*) and salt-tolerant herbs. Rush was dominated by club rush (*Ficinia nodosa*) and austral bracken (*Pteridium esculentum*). The study area was bounded by scrubby woodland habitat dominated by coast tea tree (*Leptospermum laevigatum*), coast wattle (*Acacia longifolia*) and coast banksia (*Banksia integrifolia*) (Davis *et al*. 2008). The scrubby woodland habitat was too thick to walk through and, hence, was mostly excluded from our study area. However, there were occasional thickets of coast tea tree, coast wattle and coast banksia within our study area that kangaroos sometimes rested in (Fig. 1).

Study species and population

The eastern grey kangaroo is a large, sexually dimorphic macropodid (males ≤85 kg, females ≤42 kg; Coulson 2008), which forms open membership groups of varying size (Jarman and Coulson 1989). Eastern grey kangaroos are grazers (Taylor 1983; Davis *et al*. 2008), feeding in open, grassy areas in the hours surrounding dawn and dusk (Southwell 1987; Clarke *et al*. 1989).

The population of eastern grey kangaroos in Wilsons Promontory National Park is protected from harvesting and there are no predators of adults. The population interacts frequently with humans, and individual kangaroos can sometimes be approached to within 5 m before they move away. Since July 2008, male and female adult kangaroos have been captured and uniquely marked as part of a long-term study (Gélin *et al*. 2013). Most kangaroos were captured with a hand-held pole syringe (King *et al*. 2011). Adults were marked with plastic collars (Ritchey, 40-mm wide) bearing unique symbols of a contrasting colour, and reflective eartags (Allflex, 48 × 40 mm; Fig. 2). Collars last for ~2 years (M. Festa-Bianchet, unpubl. data). The locations and reproductive status of marked individuals have been monitored since the study began. Although the population was not geographically bounded, most kangaroos exhibited strong site fidelity (King *et al*. 2015).

Study timing and approach

We conducted our study in November 2012 and May 2013. These two periods were chosen to provide one larger (spring) and one smaller (autumn) population of marked kangaroos. Weekly monitoring of the population between these two periods indicated that some marked individuals, mostly adult males, moved out of the study area after the breeding season (M. Festa-Bianchet, unpubl. data). During both study periods, we first determined the true size of the uniquely collared kangaroo population by conducting intensive searches of the study area. We then conducted walked line-transect sampling and evaluated the resulting estimates of collared-kangaroo abundance against the true collared-kangaroo population size determined during the intensive searches. The same observer (RG) conducted all field work.

True collared-kangaroo population size

To determine the true number of collared kangaroos within the study area, at the start of each study period we conducted 120-min

Fig. 2. Two collared adult female eastern grey kangaroos at Yanakie Isthmus airstrip, Wilsons Promontory National Park, south-eastern Australia. Note the collar colours, symbols and eartag combinations that uniquely identify individuals. Photo credit: G. Coulson.

searches post-dawn and pre-dusk, when kangaroos were most active, to identify collared individuals. Each search involved walking through the study area looking for kangaroos. When a kangaroo was detected, the observer approached as closely as possible without flushing the animal and used binoculars (Nikon 7294 Monarch 5, 8 × magnification, Nikon Vision Co., Tokyo, Japan) to determine whether it was collared, and if so, to identify it from its collar colour, symbol and eartag combination (Fig. 2).

The cumulative number of uniquely collared individuals detected in the study area was plotted against the number of intensive searches. In the first study period, we stopped searching when the cumulative number detected did not increase in three consecutive searches, which occurred after 10 searches (see Results). In the second study period, the cumulative number detected did not increase in three consecutive searches after nine searches; however, for consistency with the first study period, we conducted one additional search.

Walked line-transect sampling

Six parallel north–south line transects were systematically spaced at 200-m intervals across the study area (Fig. 1). The transects were marked with flagging tape on star pickets and varied in length from 441 to 962 m, with a total length of 3745 m.

Within 24 h of determining the true collared-kangaroo population size, the walked line-transect sampling began. Transects were walked at 2–3 km h^{-1}, with one or two transects being completed per morning (≤120 min post-dawn) or evening (≤120 min pre-dusk). Each transect was sampled four times in November 2012 and seven times in May 2013, with similar proportions of dawn and dusk surveys. The order in which transects were walked was randomised within each replicate to minimise any potential effect of survey order. When a collared kangaroo was sighted, the radial distance in metres to the animal was measured using a laser range finder (Bushnell Elite 1500 7 × 26 Rangefinder, Bushnell Corporation, Kansas, USA) and the bearing was measured using a sighting compass (Suunto KB-14/360R Opti-compass, Vantaa, Finland). Collared kangaroos that were flushed or seen moving at a distance were recorded at the location at which they were first seen. Because of the gregarious nature of eastern grey kangaroos, we used cluster as the object of detection, which we defined as ≥1 collared kangaroo. Cluster sizes >1 were defined as a collared kangaroo within 5 m of another cluster member in the same habitat and exhibiting similar behaviour. For clusters of more than one collared animal, the radial distance and bearing to the centre of the collared animals was measured. The habitat (grass or rush) that the cluster occupied was also recorded.

The walked line-transect data were analysed using the program DISTANCE 6.0 release 2 (Thomas *et al*. 2010, available at: http://www.ruwpa.st-and.ac.uk/distance/, verified 2 October 2015). Exploratory data analyses revealed that detection data for collared kangaroos had a long tail, so we truncated our data to exclude the furthest 5% of detections (Buckland *et al*. 2001; Thomas *et al*. 2010). Cluster size was estimated using the size-bias regression method (Buckland *et al*. 2001). Following Thomas *et al*. (2010), we evaluated the following four detection functions: (1) uniform key with cosine adjustments; (2) half-normal key with cosine adjustments; (3) half-normal key with Hermite polynomial adjustments; and (4) hazard-rate key with simple polynomial adjustments. The half-normal key with cosine adjustment, the half-normal key with Hermite polynomial adjustment and the hazard-rate key with simple polynomial adjustment models were also evaluated with habitat as a covariate using the multiple-covariate distance-sampling (MCDS) engine. We sought detection functions with high detection probability near the transect line (i.e. good shoulders), and used Akaike's information criterion (AIC) and model weights (w_i) to evaluate the relative support for each model (Akaike 1973; Burnham and Anderson 2002). Model averaging (Burnham and Anderson 2002) was used to estimate the abundance of collared kangaroos after each distance-sampling survey. One way to improve the estimation of detection functions, group size and encounter rate is to increase sample size by repeatedly walking transects within a study period (Buckland *et al*. 2001). We, therefore, cumulatively added data collected within each of the two study periods. However, the number of transects in analyses was always six.

Precision, accuracy, bias and interval coverage of estimates

For each study period, we assessed the precision of the line-transect sampling estimates on the basis of the absolute values and change of coefficients of variation (CVs) with increased sampling effort, where %CV = (standard deviation/mean) × 100 (Everitt 1998). Encounter rate was estimated by adding additional observations on each transect to those previously collected along the same transect (rather than pooling across the six transects). Both accuracy and bias have multiple definitions in the wildlife abundance-estimation literature (Hone 2008). We defined accuracy as the absolute difference between the estimated abundance of collared kangaroos and their true abundance, and assessed this using the root mean square error (RMSE; Walther *et al*. 2005; Hone 2008; Sollmann *et al*. 2015). We defined bias as the negative or positive percentage difference between the mean estimated abundance of collared kangaroos and their true abundance (Everitt 1998). Bias is, therefore, relative accuracy, which is useful for comparisons within and among studies (Walther *et al*. 2005). Finally, we assessed how often the 95% confidence intervals (CIs) for the estimated abundance of collared kangaroos included the true abundance (i.e. interval coverage); if an estimator is unbiased, then the 95% CIs will include the true value 95 times of 100 times (Dodge 2003).

Results

True collared-kangaroo population size

In November 2012, 141 collared kangaroos were detected in the study area during 10 intensive searches, with no new collared kangaroos detected during Survey 9 and 10 (Fig. 3). In May 2013, 124 collared kangaroos were detected in the study area during 10 intensive searches, with no new collared kangaroos being detected in the last four surveys (Fig. 3). These values were used as the true collared-kangaroo population sizes in subsequent analyses.

Estimates of collared-kangaroo abundance using distance sampling

In November 2012, when each of the six line transects was walked four times, a total of 553 collared kangaroos was observed in 442 clusters (Table 1). In May 2013, when each transect was walked seven times, a total of 948 collared kangaroos was observed in 728 clusters (Table 1). When transects were walked once in both study periods, the number of clusters observed exceeded the minimum 60–80 recommended by Buckland *et al.* (2001) (122 and 105 in November 2012 and May 2013, respectively; Table 1). We, therefore, estimated the abundances of collared kangaroos after the six transects were each walked once, and, thereafter, when they were walked two to four times in November 2012 and two to seven times in May 2013. Mean cluster size, after adjusting for size bias, was 1.25 (95% CI; 1.19–1.30) in November 2012 and 1.32 (95% CI; 1.20–1.38) in May 2013.

Detection histogram shape varied between the two study periods, being generally more spiked in November 2012 (Fig. S2) and having a more pronounced shoulder in May 2013 (Fig. S3). In November 2012, sighting frequencies were greater in the third and fifth perpendicular distance intervals than in the first interval (Fig. S2). However, in May 2013, sighting frequencies were greatest in the first and second perpendicular distance intervals and decreased monotonically thereafter (Fig. S3). As the number of clusters observed increased, the detection histograms had more pronounced shoulders in both study periods (Figs S2, S3). There was greater spiking in both study periods when sighting frequencies were plotted by habitat (Figs S2, S3). However, consistent with our expectations, sighting frequencies declined more rapidly with increasing perpendicular distance in the rush habitat compared with in the grass habitat (Figs S2, S3).

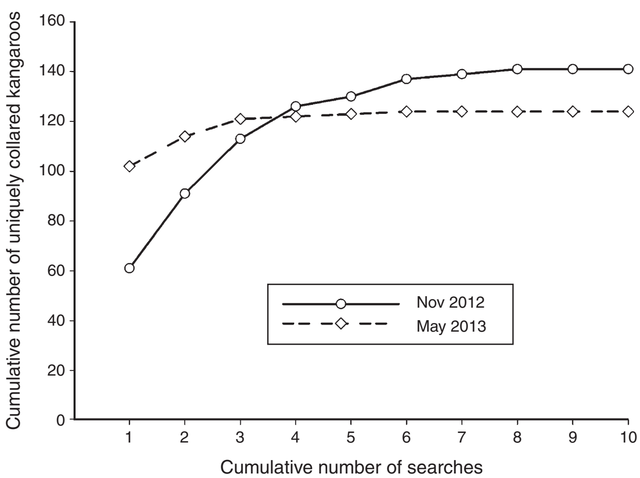

Fig. 3. Cumulative numbers of uniquely collared adult eastern grey kangaroos identified during 10 searches of the study area at Yanakie Isthmus airstrip, Wilsons Promontory National Park, south-eastern Australia, during November 2012 and May 2013.

There was often considerable model-selection uncertainty among the seven detection function models in both study periods (Tables S1, S2). Hence, there was always some support (i.e. $w_i \geq 0.05$) for models that did and did not include habitat as a covariate. After transects had been walked four times in November 2012, the best model ($w_i = 0.63$) was the Hazard rate with a simple polynomial expansion that included habitat as a covariate (Table S2). In contrast, after transects had been walked seven times in May 2013, the two best models ($w_i = 0.26$) did not include habitat as a covariate but the next two best models ($w_i = 0.15$) did include habitat as a covariate. Estimated cluster sizes changed little as sampling effort increased in both study areas (Tables S1, S2). Although there was considerable detection function model uncertainty, within each study period, the abundances (and CVs) of collared kangaroos estimated from the seven models were usually similar for a given sampling effort (Tables S1, S2).

The greatest contributor to the uncertainty in abundance estimates in both study periods was variation in encounter rates between transects, which was ≥71% in model-averaged estimates of abundance in all 11 walked line-transect sampling estimates (Tables S3, S4). Variation in detection probability (≤28%) and cluster size (≤3%) contributed much less to the precision of abundance estimates in both study periods. As the number of clusters increased in both study periods, the relative contributions of detection probability and cluster size to uncertainty in the abundance estimates decreased, and the relative contribution of encounter rate increased (Tables S3, S4).

The model-averaged estimated abundances of collared kangaroos in November 2012 changed from 154 (95%, CI: 95–250) when transects were walked once to 133 (97–183)

Table 1. Precision, accuracy and bias of walked line-transect distance-sampling estimates of the number of collared eastern grey kangaroos at Yanakie Isthmus airstrip, Wilsons Promontory National Park, south-eastern Australia

Sampling effort is the number of times that each line transect was walked. CV, coefficient of variation; RMSE, root mean square error; n.d., no data

Sampling effort	November 2012				May 2013			
	Clusters	CV (%)	RMSE	Bias (%)	Clusters	CV (%)	RMSE	Bias (%)
1	122	21.6	13.5	+9.6	105	21.6	3.0	−2.4
2	222	18.3	1.3	−0.9	210	17.6	15.2	+12.2
3	323	16.4	8.7	−6.2	319	16.8	28.4	+22.9
4	442	13.2	7.3	−5.2	402	12.6	1.1	−0.9
5	n.d.	n.d.	n.d.	n.d.	502	13.3	11.7	−9.4
6	n.d.	n.d.	n.d.	n.d.	609	14.2	11.3	−9.1
7	n.d.	n.d.	n.d.	n.d.	727	14.0	11.4	−9.2

when transects were walked four times (Fig. 4*a*). The model-averaged estimated abundances of collared kangaroos in May 2013 changed from 120 (95%, CI: 74–198) when transects were walked once to 112 (80–159) when transects were walked seven times (Fig. 4*b*).

Precision, accuracy, bias and interval coverage of distance-sampling estimates

Precision of the walked line-transect sampling estimates increased similarly with increasing sampling effort in both survey periods, from CVs of 22% when line transects were walked once to 13% after transects were walked four times (Fig. 4, Table 1). However, precision changed little when line transects were walked more than four times in May 2013.

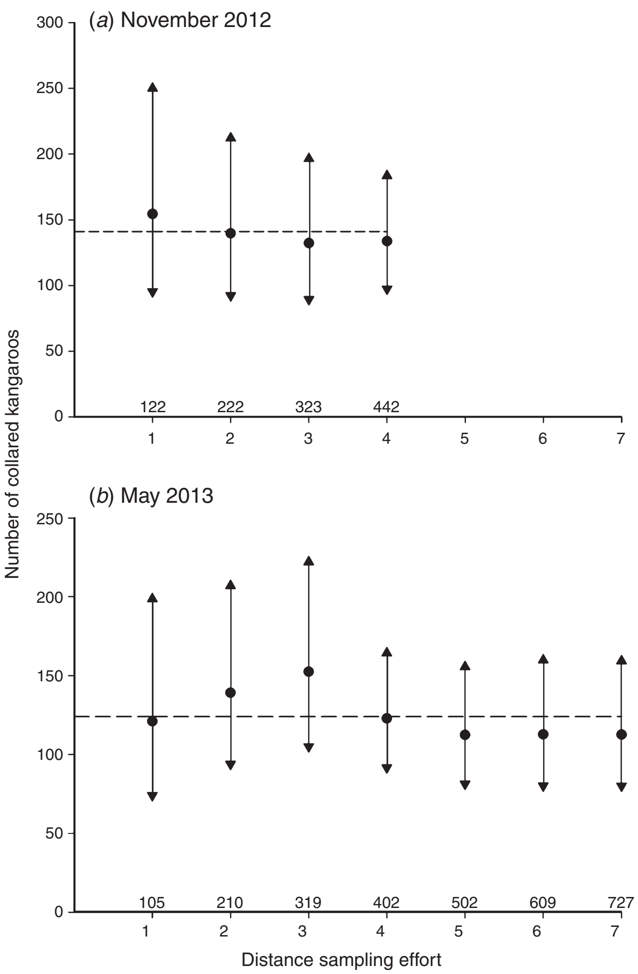

Fig. 4. Mean (solid circles) and 95% confidence intervals (vertical arrowed lines) for the number of collared eastern grey kangaroos estimated by walked line-transect sampling at Yanakie Isthmus airstrip, Wilsons Promontory National Park, south-eastern Australia, during (*a*) November 2012 and (*b*) May 2013. The true population size in each study period (141 in November 2012 and 124 in May 2013) is indicated by the horizontal dashed line, and the numbers above each *x*-axis are the clusters used in that analysis. Distance-sampling effort is the number of times that each line transect was walked. Each transect was walked four times in November 2012 and seven times in May 2013.

Walking transects twice or more always gave estimates with better precision than the recommended 20%.

The accuracy (RMSE) of the four walked line-transect sampling estimates in November 2012 varied from 1 to 13 (mean = 7.7), and bias ranged from −6.2% to +9.6% (mean = −0.7%; Fig. 4, Table 1). The accuracy of the seven walked line-transect sampling estimates in May 2013 varied from 1 to 28 (mean = 11.7), and bias ranged from −9.4% to +22.9% (mean = 0.6%; Fig. 4, Table 1). The overall mean (± s.d.) bias of the 11 walked line-transect sampling estimates was 0.1 ± 10.0%. When transects were walked four or more times in either survey period, so that precision was maximised, the bias of the walked line-transect distance-sampling estimates stabilised at between −0.9% and −9.4% of the true population sizes.

The 95% CIs of all 11 walked line-transect sampling estimates included the true collared-kangaroo population size (Fig. 4). Hence, interval coverage was achieved.

Discussion

Few studies have evaluated the precision, accuracy, bias and interval coverage of line-transect sampling estimates for unenclosed mammal populations of known size. Distance sampling along walked line transects provided precise (i.e. CV < 20%) and accurate (i.e. bias between −1% and −9%) estimates of the size of an unenclosed eastern grey kangaroo population when the number of independent clusters exceeded 400. The 95% confidence intervals for the abundance estimates always included the true abundances (i.e. interval coverage was achieved).

Previous studies evaluating walked line-transect sampling for estimating the abundance of 'wild' mammal populations have seldom presented information on how the 'true' or 'known' population sizes used for comparison with the estimate were determined. For example, Southwell (1994) evaluated walked line-transect sampling for estimating the abundance of four macropodid species at five sites in south-eastern Australia. Although various census methods were used in that study, their performance was not evaluated. We determined the number of collared kangaroos present in our study area, and, hence, available to be detected in subsequent distance-sampling surveys, in 10 intensive searches at the beginning of each of the two study periods. The form of the accumulation curves produced using this method (Fig. 3), with no new individuals detected in the last two (November 2012) or three (May 2013) searches, gives us confidence that the true collared-kangaroo population size was known with certainty in both study periods.

The relationship between sampling effort and precision of distance-sampling abundance estimates depends on many factors, and the number of observations is critical (Buckland *et al.* 2001). We always obtained precision better than the desired 20% (Buckland *et al.* 2001; Skalski *et al.* 2005) when ~200 clusters were observed (i.e. after all six transects were walked twice). Greatest precision (CV of ~13%) was achieved in both survey periods when ≥400 clusters were observed (i.e. transects were walked four times), with further sampling in the second period not increasing precision further. Precision stabilised at a CV of ~13% in both study periods because of the underlying variation in encounter rate, which was unaffected by the number of independent clusters observed. The variance of the encounter-rate estimator usually dominates the variance of abundance estimates in distance sampling, and depends on the number of transects and their lengths (Buckland *et al*. 2001; Fewster *et al*. 2009). The variance of the encounter-rate estimator can be expected to increase as the size and habitat complexity of study areas, and, hence, underlying true variation in animal density, increase.

Anderson and Southwell (1995) suggested that to be useful for wildlife management purposes, an abundance estimate should be within 10% of true abundance. Our definition of bias enabled accuracy to be compared within and between our two study periods. The bias in our estimates of collared-kangaroo abundance ranged from −9% to +23%, and interval coverage was always achieved because the 95% CIs of our estimates always included the true population size. Bias stabilised at between −1% and −9% when >400 independent clusters were observed. Line-transect sampling estimates of animal abundance may be negatively biased for three main reasons. First, animals may sometimes be unavailable for sampling. Several previous studies of the performance of walked line-transect sampling for mammals have used enclosed populations (e.g. Southwell 1994; Focardi *et al*. 2002; Porteus *et al*. 2011; Franzetti *et al*. 2012), whereas our study area was not fenced and so some collared kangaroos may have been elsewhere (hence unavailable for detection) during some distance-sampling surveys. Intensive monitoring of collared kangaroos showed that home ranges of some individuals included habitat outside our study area (W. J. King, University of Queensland, unpubl. data). Movements in and out of the study area would commonly occur in field studies because most wild populations are open (Seber 1982; Thompson *et al*. 1998; Williams *et al*. 2002). Another potential cause of kangaroos being unavailable for sampling was their habit of resting in thickets within our study area, particularly during hot weather. We attempted to minimise this possibility by walking line transects when kangaroos are most active, namely, in the 120 min post-dawn and pre-dusk (Southwell 1987; Clarke *et al*. 1989). Second, some animals may move away before they are detected. The detection histograms suggest that reactive movement was not a major cause of the small negative biases. We focused our searching on and near the transect line, so as to detect all kangaroos on the transect line before they moved. Our study population was not subject to culling and was habituated to people, resulting in some marked kangaroos moving away only when the observer approached within 5 m. Reactive movement by kangaroos in response to people walking line transects is likely to be much greater in populations subject to culling or other forms of disturbance. Third, the observer may not have counted all animals on or near the transect line because of 'counting saturation' (Southwell 1994). The densities of collared kangaroos in our study area (1.86 ha^{-1} in November 2012 and 1.63 ha^{-1} in May 2013) were similar to the densities of the tame populations sampled by Southwell (1994) and, hence, we cannot exclude the possibility that counting saturation occurred. However, we attempted to minimise counting saturation by slowly walking transects, focusing our searching on or near the transect line, and using binoculars to check for collars when kangaroos were first sighted.

Management implications

Walked line-transect sampling is widely used by wildlife managers to estimate kangaroo abundance (e.g. Southwell 1989, 1994; Southwell *et al*. 1995; Clancy *et al*. 1997; Australian Capital Territory Government 2010), including for setting cull targets for overabundant populations (Pople and Grigg 1999). Abundance estimates, therefore, need to be precise and accurate so that management actions are cost-effective and publicly defensible (Australian Capital Territory Government 2010; Parkes and Forsyth 2014). Our results showed that walking systematically-spaced line transects provides precise and accurate estimates of eastern grey kangaroo abundance, and that their 95% CIs include the true population size. However, considerably more than the recommended 60−80 observations (Buckland *et al*. 1993, 2001) were required to achieve abundance estimates with good precision (CV of <20%) and minimal (<10%) bias. Abundance estimates with precision better than 20% were always achieved with >200 observations, and bias less than 10% was always achieved with >400 observations. Walked line-transect sampling may perform less well for populations in which individuals exhibit strong reactive movement in response to people, such as populations that are hunted or culled. Following Buckland *et al*. (1993, 2001), we recommend that a pilot study always be conducted to determine the amount of sampling effort needed to attain the desired precision. Repeatedly walking line transects within a study period can greatly increase the number of observations for analysis, and may be a useful sampling strategy for small study areas and low-density populations. Provided that the key design elements and assumptions of distance sampling are met, estimates of kangaroo abundance from walked line-transect sampling can be expected to have a minimal negative bias and high precision, with 95% CIs including the true population size.

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