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Spatial patterns of kangaroo density across the South Australian pastoral zone over 26 years: aggregation during drought and suggestions of long distance movement

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Summary

1. Wildlife surveys usually focus on estimating population size, and management actions such as commercial harvesting, culling and poison baiting are referenced commonly to population size alone, without taking into account the way in which those animals are distributed. This paper outlines how point-based aerial survey data can be converted to continuous density surfaces using spatial analysis techniques. Using this approach, we describe and explore the spatial patterns of density of two species of kangaroos in an area exceeding 200 000 km^2 in South Australia over a 26-year period.

2. Densities of red and western grey kangaroos were estimated in 2 km^2 segments along aerial survey transect lines, yielding point density estimates. Universal kriging provided an unbiased interpolation of these data using the spatial autocorrelation structure described by the semi-variogram. The Getis statistic identified clusters of high and low kangaroo density.

3. Considerable year-to-year variation in the spatial patterns of kangaroo density was observed. In many cases, annual rates of increase over large areas were too high to be explained by vital rates alone, implying immigration from surrounding areas. These large shifts in distribution were occasionally to areas that had received better rainfall than the surrounding areas. For both species, there was no obvious local spatial autocorrelation pattern or clustering of kangaroo density beyond that described by average density and the present set of management regions, suggesting the latter are appropriate divisions for harvest management.

4. Data for both species fitted the power law relationship extremely well. During dry times, red kangaroos, but not western grey kangaroos, were more aggregated, supporting past ground observations at a fine spatial scale.

5. *Synthesis and applications*. Kriged density surfaces enable estimation of kangaroo density on individual properties, which are the management units at which harvest quotas or culling approvals are allocated. These estimates will be marked improvements over systematic sampling estimates when sampling intensity is low. Predictions of shifts in kangaroo distribution using rainfall or satellite imagery will allow more accurate allocation of harvest quotas. Similarly, predictions of more even kangaroo dispersion following high rainfall will allow managers to anticipate downturns in harvest rate.

Key-words: Australia, geostatistics, interpolation, kangaroos, long-term survey.

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Introduction

Whether the goal is conservation, sustainable use or pest control, wildlife management ideally requires regularly updated information on a population's size and distribution. Most frequently, population size is estimated from sample counts throughout a study area, but the pattern of distribution is either ignored or considered subjectively. Typically, management actions such as setting appropriate seasonal harvest limits or culling are triggered by estimates of the total population without sufficient regard to its spatial and temporal distribution. This means that management actions may be focused inappropriately, leading to wastage of money and outcomes that may be seriously suboptimal. Management actions would benefit from readily available and up-to-date information about the distribution of wildlife populations within a region, as well as the total population size. To do this, point-based sampling data need to be translated to density surfaces. Density surfaces modelled using geostatistics or habitat models have been produced from ground and airborne surveys of marine (e.g. Augustin *et al.* 1998; Rivoirard *et al.* 2000) and terrestrial (e.g. Campbell & Borner 1995; Rempel & Kushneriuk 2003) wildlife populations. However, few, if any, studies have modelled wildlife density over a large spatial and temporal extent, thereby providing local estimates of population size to inform more focused management actions.

We address this problem using 26 years of aerial survey data of counts of red kangaroos (*Macropus rufus*) and western grey kangaroos (*M. fuliginosus*) for the South Australian Pastoral Zone (SAPZ, 282 000 km^2) (Fig. 1). Throughout large areas of Australia's semi-arid rangelands, kangaroo populations are harvested sustainably for a meat and skin industry and, outside the prescribed harvest areas, culled under pest destruction permits (Pople & Grigg 1998). Annual harvest quotas are set as a percentage (typically 10–20%) of the most recent estimates of population size, determined usually by aerial survey, in large management regions (100 000s km^2). The problem with estimating population size for smaller management units is that, for a given survey intensity, the precision (i.e. standard error/mean × 100) of a population estimate declines with the size of the survey area. In highlighting this problem, Caughley (1979) considered a precision of 40% inadequate, but a precision of 5% useful for kangaroo management based on the ability to detect biologically significant changes in numbers over time (Caughley, Sinclair & Wilson 1977). Given a proportional harvesting strategy rather than a strategy based on population trends, improving precision is best considered as reducing the risk of under or overharvesting (McCarthy 1996; Pople 2004). Using this framework, Pople, Cairns & Menke (2003) found that the probability of quasi-extinction for a modelled, harvested kangaroo population increased dramatically above a precision of 50%. Harvest quotas can therefore be set reliably only for regions that are considerably larger than 10 000 km^2 and so precision is generally < 40%, given the sampling intensity used in aerial surveys of kangaroos (e.g. Cairns *et al.* 2000). However, operational harvest management, including in some cases the issue of harvest quotas, is at the much finer scale of a property (usually < 2000 km^2), largely on an *ad hoc* basis. This is important to management because harvest rate can vary substantially within regions because of variation in accessibility, kangaroo densities and distance to dealer sites where harvested animals must be traded (Sinclair 1977; Pople 1996).

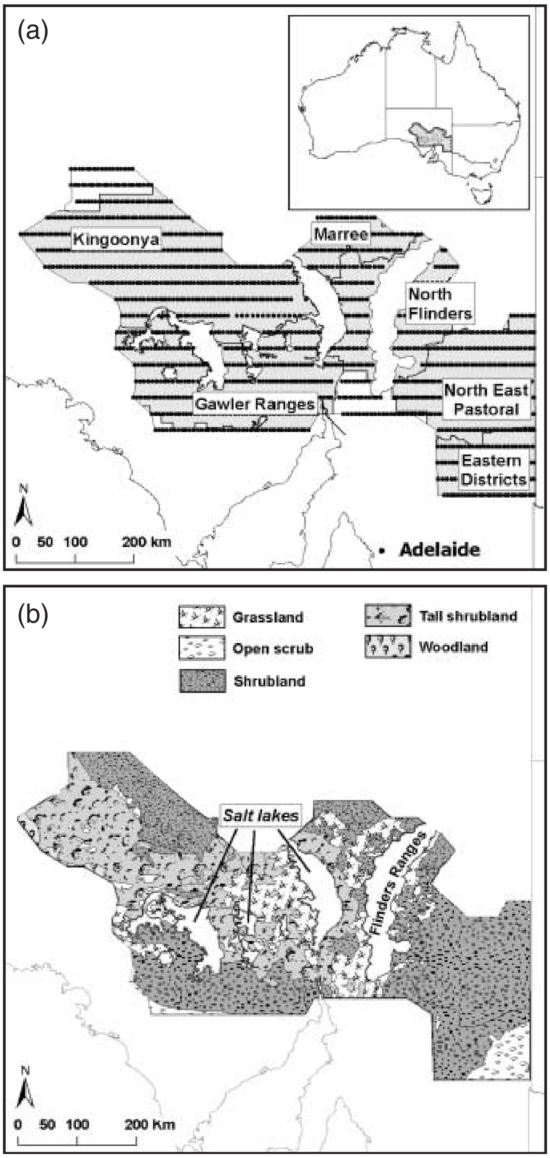

Fig. 1. (a) The South Australian pastoral zone (hatched) showing soil conservation boards (shaded) which serve as kangaroo management regions and the location of survey segments (●) in 2003. (b) Vegetation structural formations within the survey area (Boomsma & Lewis 1980).

Previous studies on kangaroo population dynamics have focused on changes in overall abundance rather than on changes in distribution, and have not been spatially explicit. Fluctuations in kangaroo numbers and their relationship with food supply have been described in a number of studies (e.g. see review by Cairns 1989; also McCarthy 1996; Cairns *et al.* 2000; Jonzen *et al.* 2005). The underlying environmental determinants of kangaroo distribution have been described similarly in studies throughout each species' range (see review by Pople 1989). However, these studies have either been conducted on such a broad scale that movement has been ignored (e.g. Caughley *et al.* 1987), or at a scale so fine that movement is a prime focus (e.g. Priddel 1988). Short time-frames also have constrained interpretation of data from most previous studies and, with the exception of Cairns, Pople & Grigg (1991), descriptions of broad-scale kangaroo distribution have typically covered only 1–3 years, limiting the generality of the results. Distribution data spanning long time-scales (decades rather than years) also allows assessment of hypotheses specific to temporal variation. Home range movements of kangaroos, especially red kangaroos, are influenced by temporally and spatially varying food availability (Norbury, Norbury & Oliver 1994; McCullough & McCullough 2000), which in turn may influence their broad-scale distribution pattern as well as their dispersion. In this context, 'pattern of distribution' refers to the geographical variation in density and 'dispersion' refers more specifically to the extent of aggregation or evenness within an area.

This paper analyses the long-term spatial variations in red and western grey kangaroo distribution for the South Australian pastoral zone. It extends the analysis of Cairns, Pople & Grigg (1991) by using a considerably longer time-series and geostatistical methods to explore patterns of distribution and annual changes in the dispersion of kangaroos at a finer scale. The resulting spatial and temporal patterns will allow kangaroo and land managers to allocate harvest quotas and interpret variation in harvest offtake more effectively. These patterns provide insights into kangaroo ecology including how kangaroo distribution and dispersion changes through wet and dry years.

Materials and methods

AERIAL SURVEY DATA

Aerial surveys of kangaroos in the South Australian pastoral zone (Fig. 1) have been conducted annually since 1978 in order to determine the size of populations and thereby assist setting harvest quotas. Survey methods and the transect lines flown have remained essentially the same as those used in the 1978 survey (Caughley & Grigg 1981; Grigg *et al.* 1999). The survey comprises a series of east–west orientated transects, 28 km apart, providing a sampling intensity of approximately 1·3% and yielding precisions of around 7% and 13% for population estimates of red and western grey kangaroos, respectively, within the entire study area (Caughley & Grigg 1981).

Transects were flown at a ground speed of 185 km h^{-1} by a high-wing aircraft (e.g. Cessna 172) at 76 m height. An observer on either side of the aircraft counted kangaroos in 200 m-wide strips along 5 km segments (i.e. 1 km^2), each separated by a 7-second break (i.e. 0·2 km) in counting. Counts were adjusted for visibility bias according to Caughley, Sinclair & Scott-Kemmis (1976) for red kangaroos and Grigg & Pople (1999) for western grey kangaroos. Counts were also adjusted where necessary for air temperatures according to Caughley (1989). Areas higher than the 500 m contour in the Flinders Ranges were not surveyed because of flying difficulties. In preparation for the modelling of continuous surfaces, each 5 km aerial survey segment was georeferenced to its midpoint by mapping segments relative to the start and finish of transects.

SELECTION OF AN APPROPRIATE INTERPOLATION TECHNIQUE

We evaluated four commonly used and commercially available interpolation techniques: kriging, splines, triangulated irregular network and inverse distance weighting (Isaaks & Srivastava 1989; Declercq 1996; Burrough & McDonnell 1998). Our requirements for interpolated surfaces pointed to an interpolator which is inexact and smoothes over individual data points. The requirement for a realistic appearance rules out triangulated irregular networks (TIN), but also inverse distance weighting (IDW), which produce counterintuitive local peaks at data points. Left with the choice of a spline or kriging approach we chose the latter, due mainly to the ability to assess the estimation errors in a kriged surface (Isaaks & Srivastava 1989). Kriging is a statistical approach free from bias, and very suitable for representing phenomena with strong random components.

SPATIAL ANALYSIS OF KANGAROO DISTRIBUTION

Kriging

Kriging was implemented using the Geostatistical Analyst extension to ArcGIS (ESRI 2004). GS+ (Robertson 2000) was used to calculate and compare semi-variograms for a range of search angles. Two forms of validation were employed to allow assessment of alternative modelled density surfaces: (1) leave-one-out cross-validation is integrated in the geostatistical software, and was used for all surfaces; and (2) setting aside every second survey point for independent comparison. Modelling of the density surfaces was guided largely by the goodness-of-fit to modelled points and the realism of the produced surfaces. The search angles were varied to produce results least biased by survey direction and environmental gradients. The search angle is the axis or axes along which autocorrelation is assessed. Universal (a combination of global and local methods) anisotropic kriging was used to estimate densities in 5 × 5 km cells for the study area. This method was used with first-order trend removal, thus superimposing the local variation over the overall trend. From these density surfaces mean density surfaces were derived to identify areas with consistently high or low kangaroo densities. Coefficient of variation

(CV) surfaces enabled areas of high and low population variability to be identified. Final modelling of density surfaces in ArcGIS was best achieved with a spherical model fitted to the semi-variogram following first-order trend removal. A 45° search angle to the survey lines appeared optimal, capturing along- and between-survey line variability. The range was constrained to be > 4·5 km.

Geostatistics

Semi-variograms (equation 1) were used to quantify spatial patterns in kangaroo distributions and provide guidance for the interpolation. These techniques have been applied extensively in the physical sciences and epidemiology, but have so far had limited application in ecological studies (Cressie 1991; Fortin 1999; Dungan *et al.* 2002; Legendre *et al.* 2002). The semi-variogram was used to express the strength of association between pairs of locations as a continuous function of the separating distance. The semi-variogram and related functions separate the large and small-scale variation in a spatial phenomenon. This was considered relevant to kangaroo management, as the areal extent, duration and frequency of many population processes such as dispersal are not fully known. The scale(s) of these processes has a bearing on the appropriateness of the survey design and the appropriate scale of harvest regulation. If geostatistics are applied to map local indicators of spatial association rather than to obtain global parameters, maps of spatial statistical characteristics of a phenomenon are obtained.

The local semivariance was calculated for densities in survey segments averaged over the study period in 5 × 5 km cells using the program VESPER (Minasny, McBratney & Whelan 2002). This enabled the spatial variation in spatial autocorrelation to be assessed. We also examined local semi-variogram parameters, such as the range to identify a threshold distance beyond which density is no longer autocorrelated.

$$\gamma(h) = \frac{1}{2m} \sum_{i=1}^{m} [Z(x_i) - Z(x_i + h)]^2 \qquad \text{eqn 1}$$

where $\gamma(h)$ = average semivariance at lag h for all data points, $Z(x_i)$ = kangaroo numbers at a sample or interpolated point, h = lag distance, m = number of observation pairs separated by lag h and i = location of sample or observation point (pixel)

The Getis statistic (G_i^*) provides a measure of the degree of aggregation of high or low values, and can be applied as a summary measure to a series of points or a continuous spatial surface (Wulder & Boots 1998). Resulting clusters can then be associated with environmental patterns, such as soil type, vegetation community, drainage catchments and areas of similar rainfall or land-use practices. The Getis statistic (equation 2) was calculated for the temporally and spatially aggregated kangaroo density data for 25 × 25 km cells for the period 1978–2003, using the program ROOKCASE (Sawada 1999).

$$G_i^*(d) = \sum W_{ij}(d) X_j \Big/ \sum X_j \qquad \text{eqn 2}$$

where $G_i^*(d)$ = Getis statistic for point i at distance d from point i, $W_{ij}(d)$ = spatial weights matrix at distance d, in two dimensions, i and j, and X_j = kangaroo numbers at a sample or interpolated point.

Taylor's power law

At a scale of 1–16 ha, red kangaroos are reported to exhibit a clumped distribution (e.g. Caughley 1964), with an increased aggregation during dry periods around remnant pasture (e.g. Newsome 1965). Soil water-holding capacity is an important factor determining remnant pasture during these periods. Kangaroos in the SAPZ are managed in regions based on district soil conservation boards (SCBs) that correspond roughly to the environmental provinces described by Laut *et al.* (1977). Six SCBs, ranging in size from 13 000 to 71 400 km^2, cover most of the survey area (Fig. 1) and were used in the analyses here. The degree of clumping in the red and western grey kangaroo populations for a 2-km^2 survey unit in each of the six SCBs was measured by the parameter b in Taylor's power law (Taylor 1961), where the variance (s^2) of a population is proportional to a fractional power (b) of the mean (m):

$$s^2 = am^b \qquad \text{eqn 3}$$

Parameters a and b were calculated from the intercept $\log_{10}(a)$ and slope(b) of a regression of $\log_{10}(s^2)$ on $\log_{10}(m)$ of the kangaroo densities in survey units within each SCB. Each year provided a single point in the analysis. Heterogeneity of slopes and differences among intercepts was assessed using an analysis of covariance. The residuals from this relationship were then correlated with rain that had fallen in the 1, 3, 6 and 12 months prior to the winter aerial survey, and with annual exponential rate of increase [i.e. $\log_e(N_{t+1}/N_t)$]. These rainfall intervals are known to correlate with pasture growth and biomass in the Australian arid zone (Robertson 1987; Wellard 1987). An alternative measure of pasture conditions to rainfall is the Normalized Difference Vegetation Index (NDVI), which is a measure of green vegetation derived from satellite multispectral image data (Tucker *et al.* 1985). A derived index is the difference between the maximum and minimum NDVI (NDVI flush) within an annual growth cycle (Cridland, Burnside & Smith 1995). The residuals from equation 3 were analysed for correlation with 6-weekly NDVI and NDVI flush data averaged over the 6 months prior to survey. Both measures were standardized over time to account for regional differences in mean rainfall and NDVI. Differences in the slope parameter (b), and therefore dispersion, between species were assessed similarly using an analysis of covariance (Crawley 2002).

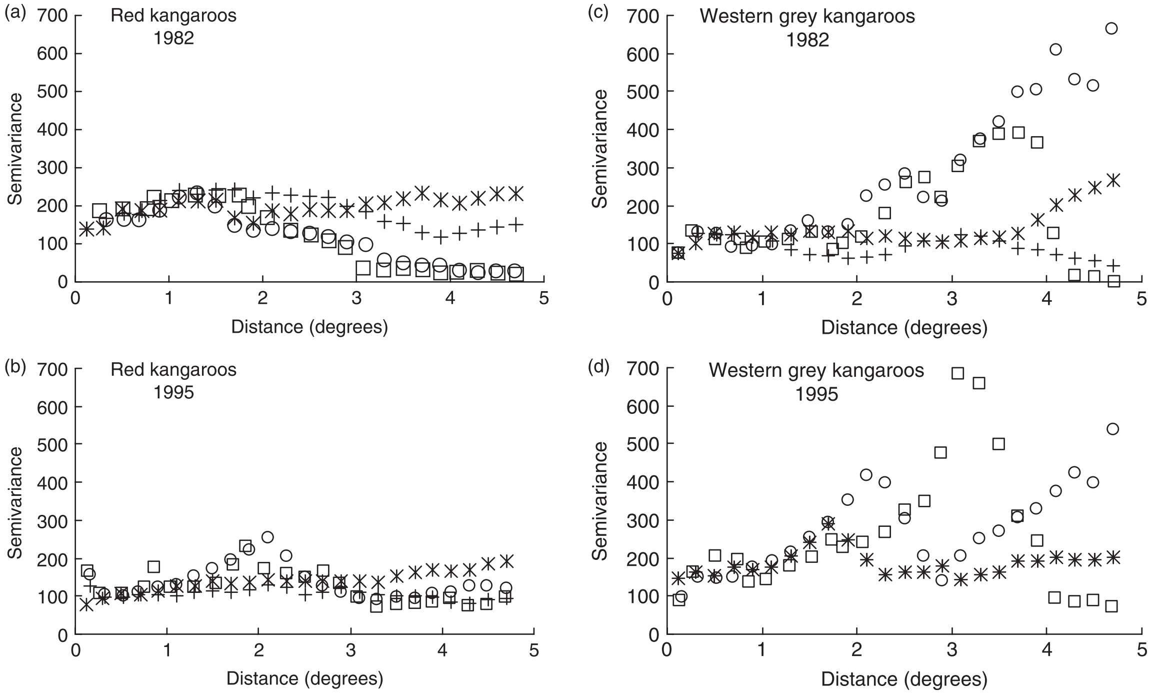

Fig. 2. Semi-variograms for: (a) red kangaroos in 1982, (b) red kangaroos in 1995, (c) western grey kangaroos in 1982 and (d) western grey kangaroos in 1995. Points represent four analysis directions (□, 0°; ○, 45°; *, 90°; +, 135°). *x*-axis units are in decimal degrees.

Fine-scale density estimation

Density of each kangaroo species was estimated using two methods for 162 properties, ranging in size from 20 km^2 to > 2000 km^2, within the six SCBs. One estimate of property-scale density was systematic sampling density D_{ss}, which is the average of the density for aerial survey units that fall within a property. An alternative estimate D_k was derived from integrating under the interpolated density surface. These two estimates were calculated for each year. For each property, bias was calculated as $\log_e(D_{ss}/D_k)$ to place the simple ratio on a symmetric scale. Defining bias in this way assumes that the interpolated density estimate is more accurate. The average bias over the 26 years was then calculated for each property and mapped. To avoid undefined values, 0·001 was added to each density estimate.

Results

KANGAROO DISTRIBUTION AND ABUNDANCE

Spatial structure

Initial exploration of the data using semi-variograms indicated distinct spatial scales of aggregation for both species, as shown in Fig. 2. The analysis of dispersion (see below) indicated that, for the study period, red kangaroos were most aggregated in the drought year of 1982 (Caughley, Grigg & Smith 1985) and most evenly dispersed in 1995, when rainfall prior to survey had been above average in most areas (mean ± SE standardized 6-months rainfall prior to survey = 0·61 ± 0·16 SD units across SCBs). In each semi-variogram (Fig. 2), the 90° directional plot provided the most detailed information, as it is parallel to the survey line. The large ranges in 1995 reflect broad-scale correlation structures that were not appropriate for interpolation here. These values were also sensitive to the interval between flight lines and the lag distance used in their calculation. The steadily increasing variance for western grey kangaroos is a regional trend caused by their restriction to the southern part of the study area.

Figure 3 shows annual variation in the semi-variogram range and kangaroo density over the study period, with 1991–4 having a notably lower range than other years for red kangaroos, while the mid-1980s and mid-1990s had higher values for western greys. Significant seasonal variations in spatial patterns of kangaroo density were evident from the fluctuating range values (14–97 km for red kangaroos, 13–63 km for western grey kangaroos). There was also considerable spatial variation in the local range for both species, without obvious spatial clustering (Fig. 4, Table 1).

Spatial and temporal pattern

The summary maps of long-term mean density, coefficient of variation in density, Getis G_i^* and local variogram range for the two kangaroo populations show a different pattern. High positive (negative) values of the Getis statistic indicate clustering of high (or low) kangaroo numbers (Fig. 5). Highest and most stable densities for red kangaroos are in the north-east SAPZ (Figs 6a and 7a),

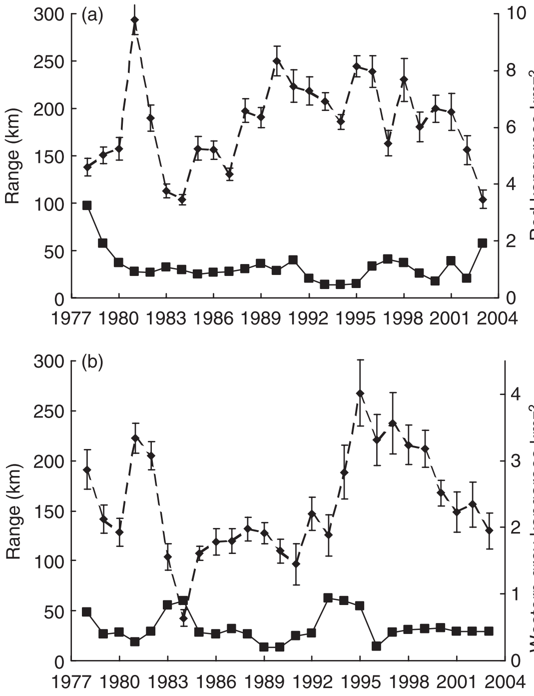

Fig. 3. Semi-variogram range (■) and population densities (◆) (± SE) for 1978–2003 for: (a) red kangaroos and (b) western grey kangaroos within the study area.

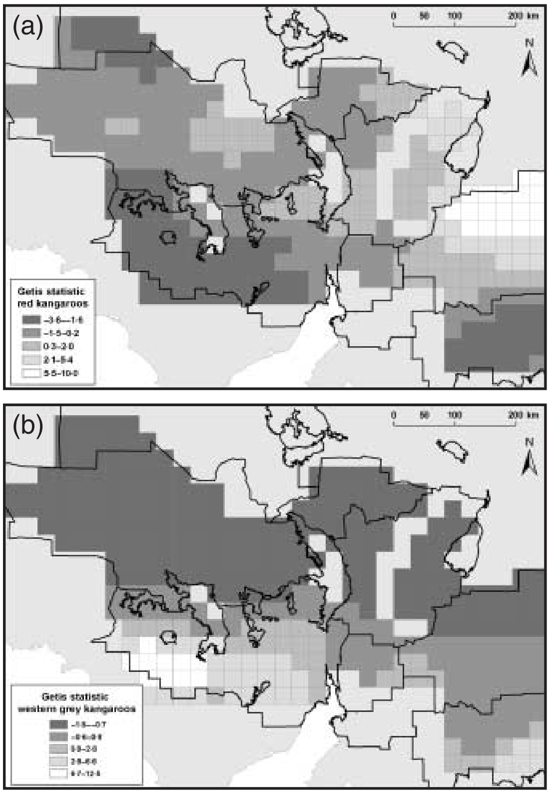

Fig. 5. The Getis statistic for: (a) red and (b) western grey kangaroo density, averaged over 1978–2003 within 25 × 25 km cells, in the South Australian pastoral zone.

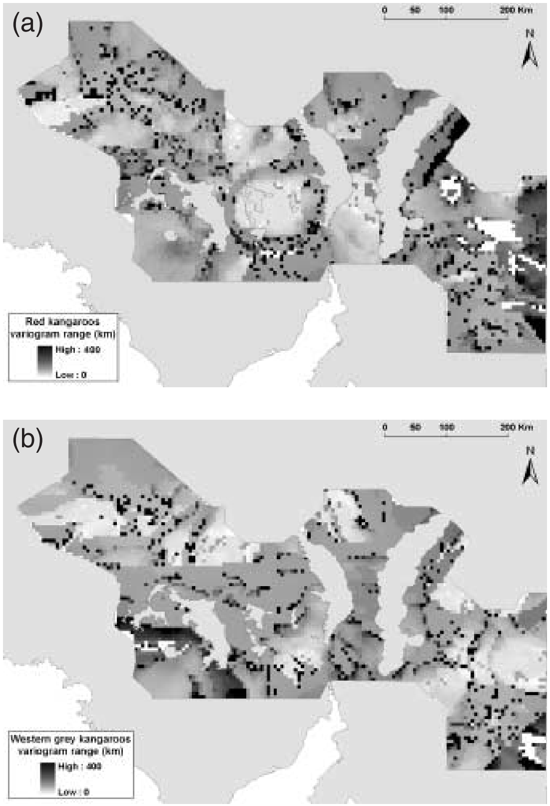

Fig. 4. Map of local semi-variogram range for: (a) red kangaroo and (b) western grey kangaroo density, averaged over 1978–2003 within 5 × 5 km cells, in the South Australian pastoral zone.

Table 1. Parameters, coefficients of determination (r^2) and models for the semi-variograms shown in Fig. 2

	Red kangaroo		Western grey kangaroo	
	1982	1995	1982	1995
Range (degrees)	0·43	0·50	0·27	1·70
Nugget	107·6	67·4	24·1	117·9
Sill	215·3	134·9	113·6	235·9
r^2	0·75	0·47	0·73	0·71
Model	Exponential	Spherical	Exponential	Spherical

while highest and most stable densities of western grey kangaroos are in the Gawler Ranges and south-east SAPZ, where red kangaroo densities were low (Figs 6b and 7b). Both species show most marked fluctuations at the edge of their ranges, although this is exaggerated because of zeros in low-density areas inflating the coefficient of variation. The spatial clustering of temporally averaged low and high densities of both species, as indicated by the maps of G_i^* (Fig. 5a,b), mirrored the maps of average, interpolated density over the study period (Fig. 6).

Across the entire SAPZ, numbers of both species fluctuated over a broad range for the 26-year study period (Fig. 3). The time-series included two periods of drought (1982–3 and 2002–3), when numbers declined markedly. In 1982 and 1983, mean ± SE standardized

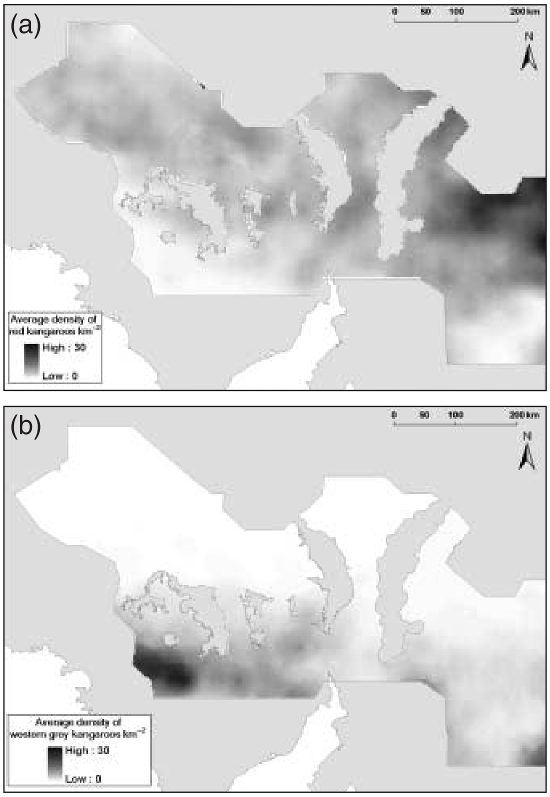

Fig. 6. Average density of: (a) red kangaroo and (b) western grey kangaroos in the South Australian pastoral zone over 1978–2003. Density surfaces are calculated from annual densities in 5 × 5 km cells interpolated from densities in aerial survey segments (Fig. 1a) using universal kriging.

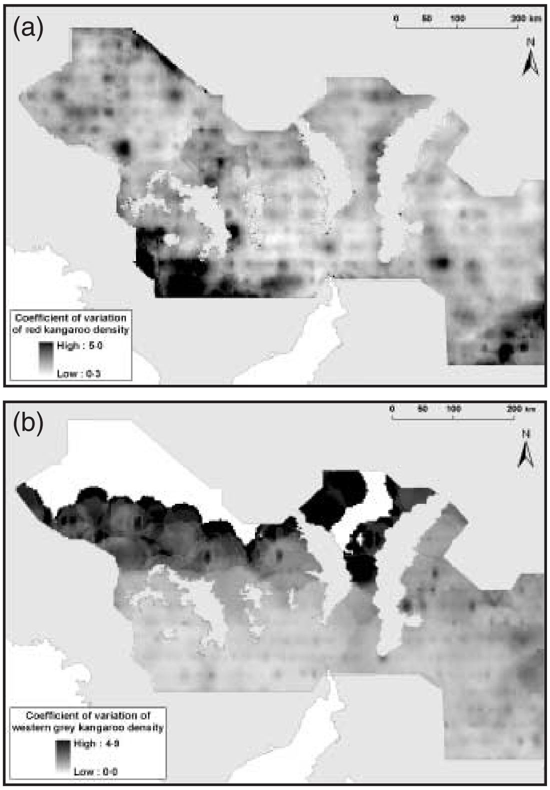

Fig. 7. Coefficient of variation of: (a) red kangaroo and (b) western grey kangaroo density over 1978–2003. Calculated from annual densities in 5 × 5 km cells interpolated from densities in aerial survey segments (Fig. 1a) using universal kriging.

rainfall 12 months prior to survey was –0·67 ± 0·07 and –1·45 ± 0·10 SD units, respectively, across all SCBs and in 2002 and 2003 rainfall was –0·49 ± 0·14 and –0·64 ± 0·10 SD units, respectively. Changes in patterns of kangaroo distribution over time as shown in the coefficient of variation maps (Fig. 7) reflect the spatially dynamic nature of the system. One way of displaying this changing pattern of distribution is to map the annual exponential rate of increase of kangaroos. In some areas and in some years, the rapid increase in numbers over large areas cannot be explained by recruitment and survival alone. This suggests an important role for movement in broad-scale population dynamics. Figure 8a shows an interpolated surface for the exponential rates of increase for red kangaroos for the period 1986–7. In the eastern SAPZ, there was a large, contiguous area where red kangaroo numbers more than tripled. This change occurred over a large area, and within contiguous blocks; was surrounded by coincident declines in red kangaroo numbers; and was also visible in the original survey data. Together this indicates movement of large numbers of red kangaroos over distances greater than 50 km. The areas of rapid population increase in the east coincided partially with areas receiving above average rainfall in the six months prior to the aerial survey in 1987 (Fig. 8b). However, the correlation between rainfall and rate of increase across the study area is not significant ($r = –0·02$, $n = 340$) at the resolution of 25 km.

KANGAROO DISPERSION

For red kangaroos, the most parsimonious regression model ($r^2 = 0·90$) describing Taylor's power law included shared, rather than separate slopes ($F_{5,144} = 0·80$, $P > 0·5$), but separate intercepts for each SCB ($F_{5,149} = 11·83$, $P < 0·001$), indicating constant degree of aggregation ($b = 1·50 \pm 0·06$) across SCBs (Fig. 9). Points for the higher rainfall SCBs in the southern pastoral zone fell along regression lines elevated from the other SCBs. This was reflected in a larger estimate for the intercept parameter (a in equation 3) and a simpler model with two intercepts ($F_{4,149} = 1·35$, $P > 0·2$). The residuals from this relationship were not correlated with rate of increase, but correlated negatively to all rainfall and NDVI measures; most strongly to rain falling 12 months prior to survey ($r = –0·32$, 95%CI: –0·45, –0·17). The relationship has considerable scatter, but the absence of points at high rainfall and large positive residuals (= highly aggregated) was notable. Low rainfall frequently, but not always, leads to greater aggregation, but the population was always more evenly dispersed following

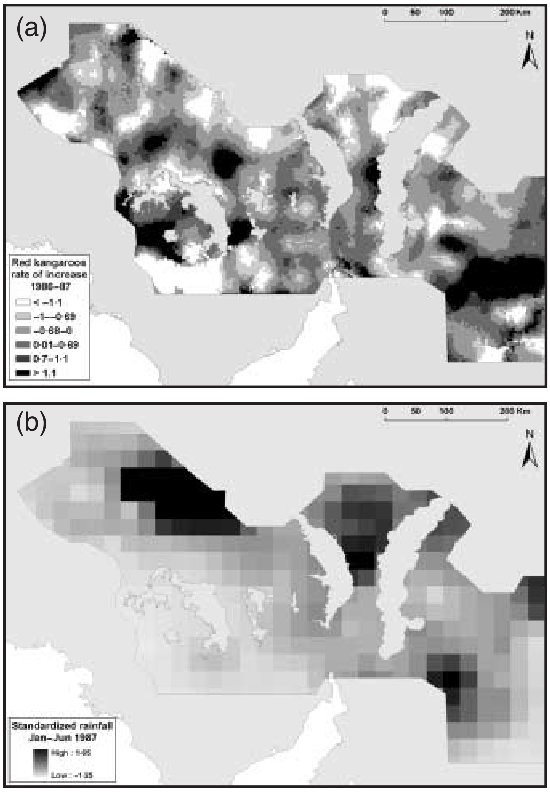

Fig. 8. (a) Annual exponential rate of increase for red kangaroos over 1986–87. Calculated from annual densities in 1986 and 1987 in 5 × 5 km cells interpolated from densities in aerial survey segments (Fig. 1a) using universal kriging. (b) Rainfall, standardized using the long-term mean and standard deviation, for January–June 1987. Rainfall surfaces were first interpolated using inverse distance weighting from Bureau of Meteorology data recorded at stations throughout the study area.

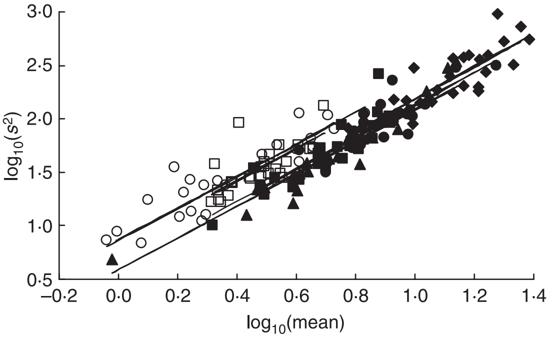

Fig. 9. Relationship between $\log_{10}$ (variance) and $\log_{10}$ (mean) of red kangaroo density in six soil conservation boards (see Fig. 1a) for each year over 1978–2003. Fitted regression lines with a common slope are also shown. Eastern Districts (○), Gawler Ranges (□), Kingoonya (■), Marree (●), North Flinders (▲), North-east Pastoral (◆).

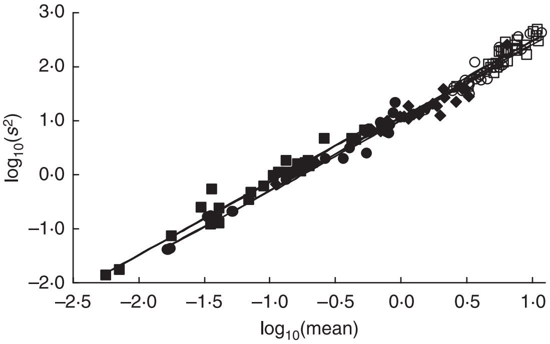

Fig. 10. Relationship between $\log_{10}$ (variance) and $\log_{10}$ (mean) of western grey kangaroo density in six soil conservation boards (Fig. 1a) for each year over 1978–2003. Fitted regression lines with a common slope are also shown. Eastern Districts (○), Gawler Ranges (□), Kingoonya (■), Marree (●), North Flinders (▲), North-east Pastoral (◆).

widespread high rainfall. These results are reflected in the temporally and spatially varying semi-variogram range (Figs 3 and 4), although patterns of dispersion did not necessarily coincide with autocorrelation patterns.

For western grey kangaroos, there was some suggestion of heterogeneity of regression slopes among SCBs ($F_{4,117} = 2{\cdot}16$, $P = 0{\cdot}07$) due to less aggregation in the North-east Pastoral SCB. However, the most parsimonious model ($r^2 = 0{\cdot}98$) again included only separate intercepts for each SCB ($F_{4,121} = 6{\cdot}63$, $P < 0{\cdot}001$), indicating constant degree of aggregation ($b \pm \mathrm{SE} = 1{\cdot}35 \pm 0{\cdot}03$) across SCBs (Fig. 10). In contrast to red kangaroos, the residuals from this relationship were not correlated with rate of increase or any rainfall or NDVI measures. Excluding Marree SCB and examining both species together, analysis of deviance indicated little support for slopes varying among species ($F_{1,241} = 0{\cdot}74$, $P > 0{\cdot}3$), SCBs or an interaction between the two. The most parsimonious model ($r^2 = 0{\cdot}98$) included a common slope ($b \pm \mathrm{SE} = 1{\cdot}37 \pm 0{\cdot}03$) and, hence, a similar level of aggregation across SCBs for both species.

FINE-SCALE DENSITY ESTIMATION

Throughout the six SCBs, density from aerial survey could not be estimated on 28 typically small properties, because they contained no survey segments (Fig. 11a,b). Bias was correlated positively with logged property size for reds ($r = 0{\cdot}43$, $P < 0{\cdot}01$) and western greys ($r = 0{\cdot}56$, $P < 0{\cdot}01$). For both species, interpolated densities were in general higher than those based on survey segments, with a mean bias (± SE) over 1978–2003 of $-0{\cdot}73 \pm 0{\cdot}10$ (median = $-0{\cdot}23$) for red kangaroos (Fig. 11a) and $-0{\cdot}98 \pm 0{\cdot}09$ (median = $-0{\cdot}66$) for western grey kangaroos (Fig. 11b). This negative bias was offset by a positive bias on properties with high-density segments. There was no obvious spatial pattern in the bias for red kangaroos, but segment-based (D_{ss}) densities of western grey kangaroos were consistently lower than interpolated density estimates (D_k) through the central SAPZ, the northern extremity of the western grey kangaroo range (Fig. 4b).

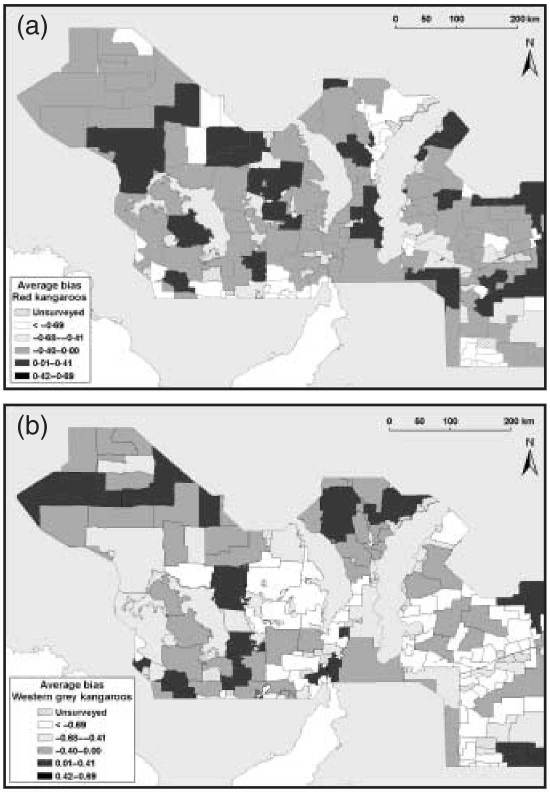

Fig. 11. Average bias over 1978–2003 in segment-based (Fig. 1a) densities of (a) red kangaroos and (b) western grey kangaroos in properties within the South Australian pastoral zone. Bias was calculated as the $\log_e(D_{ss}/D_k)$, where D_{ss} is density based on systematic sampling and D_k is density based on an interpolated density surface. 0·001 has been added to densities to avoid undefined values.

Discussion

The primary aim of this study was to employ a range a geostatistical tools to analyse long-term spatial patterns and variations in kangaroo distribution as a basis for improving the spatial scale of kangaroo management in the South Australian pastoral zone. Kriging allowed a detailed exploratory analysis of spatial pattern within the point data set. In combination with the ability to assess or map the likely error in the kriged surfaces, this interpolation technique was inherently suited to exploring and mapping spatial patterns in wildlife survey data and, perhaps, modifying survey design to improve the accuracy and precision of estimates. Thus, high density areas and areas with large error could be surveyed with increased sampling intensity and, conversely, sampling could be reduced in areas of uniformly low density.

SPATIAL–TEMPORAL PATTERNS

Conversion of point-based samples from long-term, frequent, systematic surveys to a spatially extensive map of population density enables recurrent patterns in the distribution of animals to be clearly identified. The results show that the broad pattern of distribution of both red and western grey kangaroos in the SAPZ was relatively stable over the study period. High densities of red kangaroos were recorded consistently in the north-east of the SAPZ, an area with a mosaic of soil and vegetation types, but dominated in general by low bluebush shrublands and calcareous soils and where sheep are grazed at a relatively high density (Cairns, Pople & Grigg 1991). Western greys are restricted to the less arid parts of the study area and densities were consistently high in the south-west. This area is also heterogeneous in terms of soil, landform and vegetation, with many areas of woodland interspersed with grassland and open shrubland (Cairns, Pople & Grigg 1991). There is temporal variation in this pattern for both species, particularly where they occur at relatively low density (Fig. 5). This probably reflects the vagaries of marginal habitat, despite the inflation of the CV by more frequent zero observations. Whether these areas with highly fluctuating densities experience high rates of local extinction and recolonization, or are driven just by local population dynamics, or whether the high coefficient of variation is due to the interaction of low density and sampling design, is unclear from these data.

From year-to-year there were also substantial shifts in kangaroo distribution, which cannot be explained by birth and death alone. Even an unstable age distribution and biased sex ratio, possible in or after drought, can result in an annual exponential rate of increase < 0·69 in the population size (Bayliss 1985; Pople 1996). This rate is well short of the increases identified here for large areas of the SAPZ. Cairns, Pople & Grigg (1991) reported a shift in the distribution of red kangaroos during the 1982–3 drought. This was due largely to spatial variation in the onset of drought, which was delayed in the west of the pastoral zone, and resulted in spatially uneven declines in density. Uneven changes in density resulting in changes in distribution can be particularly marked during declines because of the convex shape of the numerical response of kangaroos (Davis, Pech & Catchpole 2002). What became apparent with a re-analysis of these data and over a longer time period was that distribution shifts were also associated with increases in regional density.

Long distance movements of > 100 km have been recorded for individual red kangaroos from tagging and radio telemetry (Bailey 1971; Bailey & Best 1992). However, these have been considered exceptions in a generally sedentary population where individuals move within home ranges of variable size (McCullough & McCullough 2000). Adult red kangaroos have been recorded ranging more widely during drought (Norbury, Norbury & Oliver 1994), and movements of up to 30 km have been reported for red kangaroos in response to patchy rainfall during prolonged dry spells, resulting in geographical shifts of the population (Newsome 1971; Denny 1980; Priddel 1987; Croft 1991).

The data presented here lends support to the hypothesis that large-scale movements occur to areas of potentially higher quality food supply. However, Priddel, Wellard & Shepherd (1988) and Bayliss (1985) considered red kangaroo movement had little influence on their dynamics at a scale of 440 km^2. However, the results of this study provide evidence for the existence of long-distance movement, and that populations are not closed at this scale or even at smaller scales. This apparent discrepancy from previous studies may be due to a number of factors including: the relatively short time-frame and small spatial scale of many radio-tracking and tagging studies, site-specific factors such as fences and lakes which influence movement, low recapture rates of some population classes in tagging studies and a bias towards selection of adult animals in radio tracking studies.

The exceptional fit of these data to Taylor's power law is not surprising, given its fit to a broad range of taxa (Taylor, Woiwod & Perry 1978; Taylor & Woiwod 1982). A slope of between 1 and 2 has also been found for most species. We do not offer an explanation for this scaling relationship; rather, we highlight its ability to detect increased aggregation of red kangaroos during dry times, supporting fine-scale observations. What is interesting was that increased aggregation was detected here at the scale of a 2-km^2 survey segment. This suggests that seasonal movements can be detected with broad-scale aerial survey and that the more extensive NDVI data may be able to predict movement and the resulting changes in spatial distribution of kangaroos.

These seasonally variable distribution patterns have important implications for management. Annual harvest quotas are based on surveys conducted at least 6 months prior to the actual harvest, by which time the geographical variation in kangaroo density may have altered. Spatial allocation of quotas needs to account for seasonal shifts in the spatial dispersion of kangaroos and the results here suggest this may be possible. Harvest rate appears to be influenced by spatial dispersion of kangaroos with increased harvests when animals are aggregated (Kirkpatrick & Amos 1985). Rainfall or NDVI could be used to predict downturns in harvest offtake, although the direct link between harvest rate and rainfall or NDVI needs to be quantified for the SAPZ, western New South Wales and Queensland.

APPROPRIATE SCALE OF MANAGEMENT AND ANALYSIS

A semi-variogram range of 13–97 km indicates that spatial autocorrelation needs to be accommodated in spatial modelling with data collected within these distances. The correlation structure can be incorporated directly into the model (Guisan & Zimmerman 2000; Keitt *et al.* 2002) or data can be pooled into larger units that are less likely to be autocorrelated (Buckland & Elston 1993).

Appropriate geographical stratification of regional-scale data has been considered critical for monitoring population trends in declining populations (Villard & Maurer 1996). Similarly, it will be important for other management fields such as regulating harvests. For both species, G_i^* broadly matches average density, which tends to cluster and differ in value for each SCB, providing support for this level of current kangaroo management in South Australia. Management activities such as harvest regimes, survey frequency and enforcement could be tailored to the new strata identified here. At present these activities, including the proportion of the population that is offered as a harvest quota, are undertaken uniformly or applied across SCBs within the SAPZ (SADEH 2002). However, harvest rate and variability differs among as well as within these SCBs (Jonzen *et al.* 2005), suggesting that management would be more efficient if it varied its activities accordingly (Pople, Cairns & Menke 2003; Pople 2004). The lack of clustering in the local semi-variogram range suggests that there is no need to use population management units other than the present management SCBs.

In South Australia, kangaroo harvest quotas are allocated to individual properties. More widely within Australia, permits for culling are given to individual properties. Ideally, this requires fine-scale estimates of density, relative or absolute, to divide a regional quota among constituent properties, or to assess requests for culling permits by a property manager. An obvious method for estimating density on an individual property is ground survey, but these are just not feasible on such a broad scale as the SAPZ (Caughley & Grigg 1981). This study highlights how kriging can overcome the imprecision and bias associated with low sampling intensities when estimating density on a fine scale. The marked differences between interpolated densities and averaged segment densities within properties highlights the gains that can accrue by taking the approach we have described in this paper.

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