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Estimating deer abundance from line transect surveys of dung: sika deer in southern Scotland

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Summary

1. Accurate and precise estimates of abundance are required for the development of management regimes for deer populations. In woodland areas, indirect dung count methods, such as the clearance plot and standing crop methods, are currently the preferred procedures to estimate deer abundance. The use of line transect methodology is likely to provide a cost-effective alternative to these methods.
2. We outline a methodology based on line transect surveys of deer dung that can be used to obtain deer abundance estimates by geographical block and habitat type. Variance estimation procedures are also described.
3. As an example, we applied the method to estimate sika deer *Cervus nippon* abundance in south Scotland. Estimates of deer defecation and length of time to dung decay were used to convert pellet group density to deer density by geographical block and habitat type. The results obtained agreed with knowledge from cull and sightings data, and the precision of the estimates was generally high.
4. Relatively high sika deer densities observed in moorland areas up to 300 m from the forest edge indicated the need to encompass those areas in future surveys to avoid an underestimate of deer abundance in the region of interest.
5. It is unlikely that a single method for estimating deer abundance will prove to be better under all circumstances. Direct comparisons between methods are required to evaluate thoroughly the relative merits of each of them.
6. Line transect surveys of dung are becoming a widely used tool to aid management and conservation of a wide range of species. The survey methodology we outline is readily adaptable to other vertebrates that are amenable to dung survey methodology.

Key-words: abundance estimation, dung surveys, line transect sampling, wildlife management.

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Introduction

Knowledge of population size and population structure is essential for the development of effective management strategies for deer populations. Methods employed to obtain such information are classified as broadly direct or indirect. Direct methods, such as aerial surveys (Bear *et al*. 1989; White *et al*. 1989; Trenkel *et al*. 1997) and vantage point counts (Ratcliffe 1987), are based on surveys or counts of the animals and allow estimation of the number of deer of each sex. Depending on the time of year when surveys are carried out, the number of calves can also be estimated. Indirect methods, which are usually based on faecal pellet counts (Rogers, Julander & Robinette 1958; Mitchell, Staines & Welch 1977; Bailey & Putman 1981; Putman 1984), only give an estimate of the overall deer abundance, although the approximate sex and age structure of the population can be established from visual observations, cull data and animals found dead. A further difference between direct surveys of animals and indirect surveys of dung is that the latter provide estimates of average abundance over several months, whereas the former usually yield estimates of abundance for the day of the survey, which may provide misleading information on habitat use.

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The suitability of any given method will depend on the ecology and behaviour of the species of interest, the management questions to be answered, and the type of habitat the deer inhabit.

In extensive open ground areas, both direct and indirect count methods can be used, although the former are generally more effective and widely used. In woodland areas, however, direct methods are often not feasible or they are potentially biased (Ratcliffe 1987; Buckland 1992), and indirect methods are preferred. Currently two indirect faecal pellet group methods are applied to woodland deer populations in Scotland: the 'clearance plot' method, which is based on the number of pellet groups deposited within sample plots that were initially cleared of all pellets; and the 'standing crop' method, in which all pellet groups within the sample plots are counted. Both methods require knowledge of defecation rate and length of time to dung decay in order to estimate deer density from the pellet group counts. For the clearance plot method, if no pellets decay during the time interval between clearing and counting, then only an estimate of defecation rate is required to estimate deer density.

The clearance plot method will generally provide more accurate estimates of absolute abundance than the standing crop method. However, unless there are enough resources to survey a large number of plots, the method may result in abundance estimates with poor precision in areas of low deer density, as a large number of plots may contain zero pellets (Buckland 1992). The standing crop method is thus more cost effective and yields more precise estimates of abundance for fixed resources in such circumstances. However, both methods require the detection of all pellet groups located within the sample plots, and thus are time consuming. By selecting long narrow plots, say 1–2 m wide, the task of systematically searching the plots is made easier, as a given plot can be covered in a single sweep from one end to the other. This then becomes a strip transect survey (Buckland *et al.* 1993). On the other hand, as the proportion of edge to area is relatively large for such plots, more pellet groups are located near or on the edges, and clear rules for determining whether a given pellet group is in the plot must be defined if bias is to be avoided. An alternative approach that is potentially more efficient and less prone to bias is the use of line transect methods (Buckland 1992, 1993).

In line transect sampling, the number of pellet groups located within the area surveyed is modelled as a function of the perpendicular distances of detected pellet groups from the transect line. As it is no longer necessary to detect all pellet groups within the plot, a wider strip can be surveyed and thus any potential bias from edge effects is reduced. The downward bias associated with strip transect methods when not all pellet groups within the strip are detected is also avoided. The cost of line transect sampling is that distances of detected pellet groups from the transect line must be measured.

In this paper we outline a methodology based on line transect surveys of dung that can be used to estimate deer abundance in woodland areas. As an example, we applied the method to estimate sika deer *Cervus nippon* Temminck abundance in south Scotland, and also to obtain deer density estimates by geographical block and habitat type.

Methodology

In line transect sampling an observer counts the number n of objects seen while traversing a predetermined line of length L. In the context of this paper, 'objects' refer to dung pellet groups. The perpendicular distance of each object from the transect line is also recorded. When all objects located on the line are detected with certainty, the density of objects in the area surveyed (D) is estimated as (Buckland *et al.* 1993):

$$\hat{D} = \frac{n \cdot \hat{f}(0)}{2L} \qquad \text{eqn 1}$$

The parameter $f(0)$, estimated by $\hat{f}(0)$, corresponds to the probability density function of the perpendicular distances, evaluated at zero. $f(0)$ is more readily interpreted as $1/\mu$, where μ corresponds to the perpendicular distance from the transect line within which the number of undetected objects is equal to the number of objects that were detected beyond it. μ is termed the effective strip half-width and, when multiplied by $2L$, gives the effective area surveyed.

Note that equation 1 can be conveniently rearranged as:

$$\hat{D} = \frac{n}{L} \cdot \hat{f}(0) \cdot \frac{1}{2} \qquad \text{eqn 2}$$

so that now density estimates can be easily obtained from estimates of $f(0)$ and encounter rate (n/L).

Survey design

A comprehensive overview of survey design and data recording requirements in the context of line transect sampling is given by Buckland *et al.* (1993). A key component in the design of line transect surveys is to ensure an equal coverage probability throughout the region, to reduce any bias that could result from the systematic coverage of areas that present either very high or very low deer densities. An example of a poor design might be the placement of transect lines running along contour lines, which can lead to poor precision if deer density varies with altitude. If valleys or ridges in the survey region predominantly follow a common orientation, transect lines may be placed approximately perpendicular to this orientation, for example by defining a grid of parallel lines and placing it at random over the survey region while retaining the desired orientation (perpendicular to contours). If, on the other hand, the survey region is large enough that topographic features do not have a predominant orientation, random orientation and placement of a grid of lines across the region

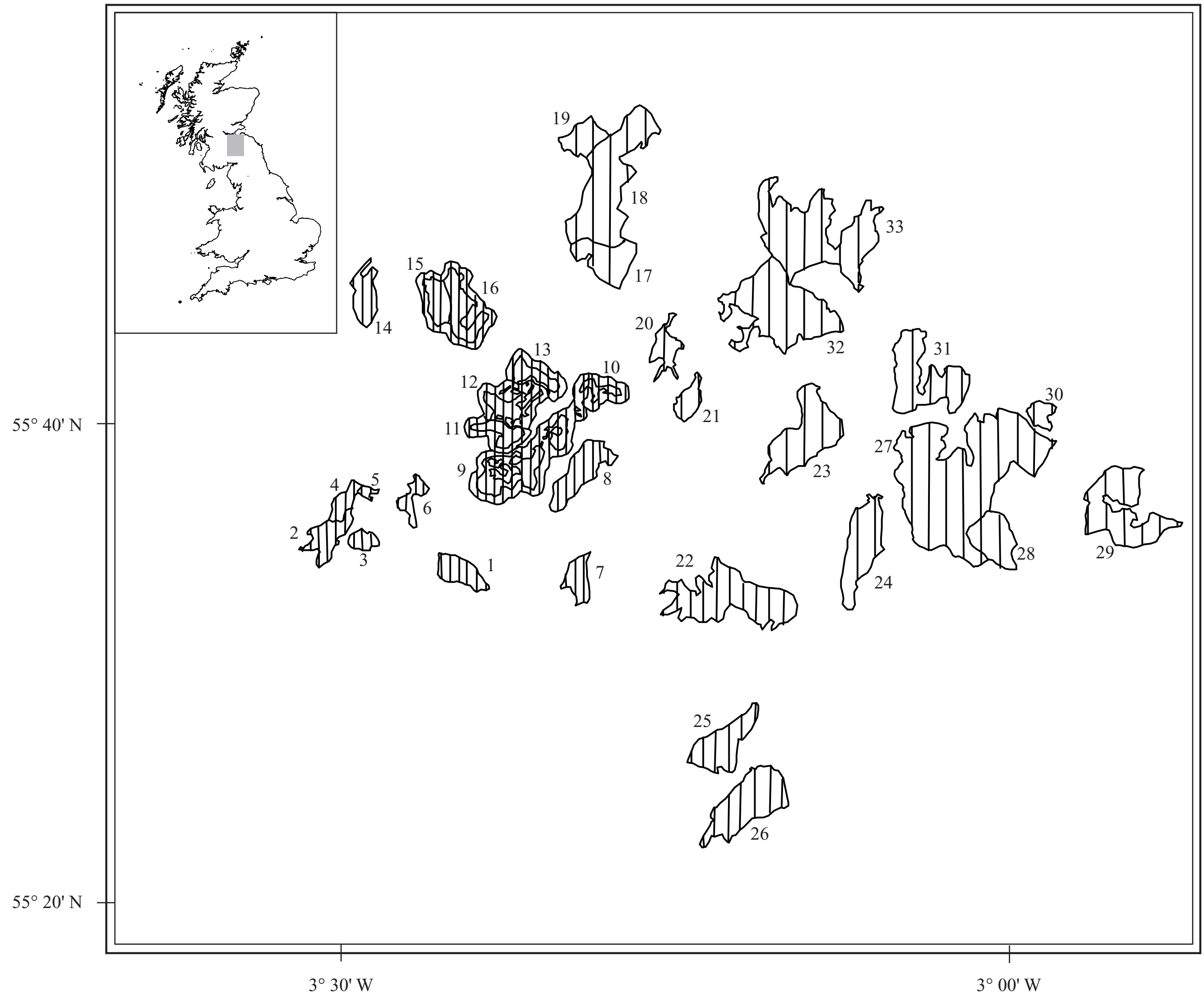

Fig. 1. Map of Peeblesshire region showing forest blocks surveyed (1–33). Also shown is the north–south grid of orientation lines along which transects were placed. For details of the spacing between lines and between transects along the lines, see the main text.

provides representative samples of the various deer densities throughout the area. For convenience, orientation might be determined by a map grid, so that lines run north–south, or east–west (e.g. Fig. 1). A zig-zag design is sometimes used to avoid dead time between the end of one transect and the start of the next (e.g. Fig. 2). To maximize the spatial coverage, transects can be placed at intervals along the line (Fig. 3). In the case of lines placed according to a grid, the distance between lines can be made equal to the distance between transects along the lines, as this allows the short lines to be treated as the sampling units, which yields more reliable estimates of variance. The choice of distance will depend on the available effort and the size of the region.

Estimates of deer abundance at a regional scale are generally required for management purposes. However, to proportion culls between landowners, estimates by geographical blocks, possibly corresponding to estates, are also needed. It can also be useful to estimate deer density for each habitat type. In addition, the probability density function of the observed perpendicular distances is likely to vary according to habitat type, and stratified analyses may be needed. Where density estimates by habitat type are needed, lines should be placed in a way such that enough effort is allocated to each habitat type. If habitat data are not available prior to the survey, unbiased estimates of abundance by habitat type can be obtained provided the design ensures equal coverage probability throughout the survey region.

Pilot surveys are recommended when prior knowledge of the expected densities in the region of interest is limited, so that results from these surveys can be used to estimate the amount of survey effort required to achieve the desired level of precision on abundance estimates. Once total transect length has been determined, many short transect lines are preferred over a few long ones, because they give better spatial coverage and more reliable estimates of precision. In the case of

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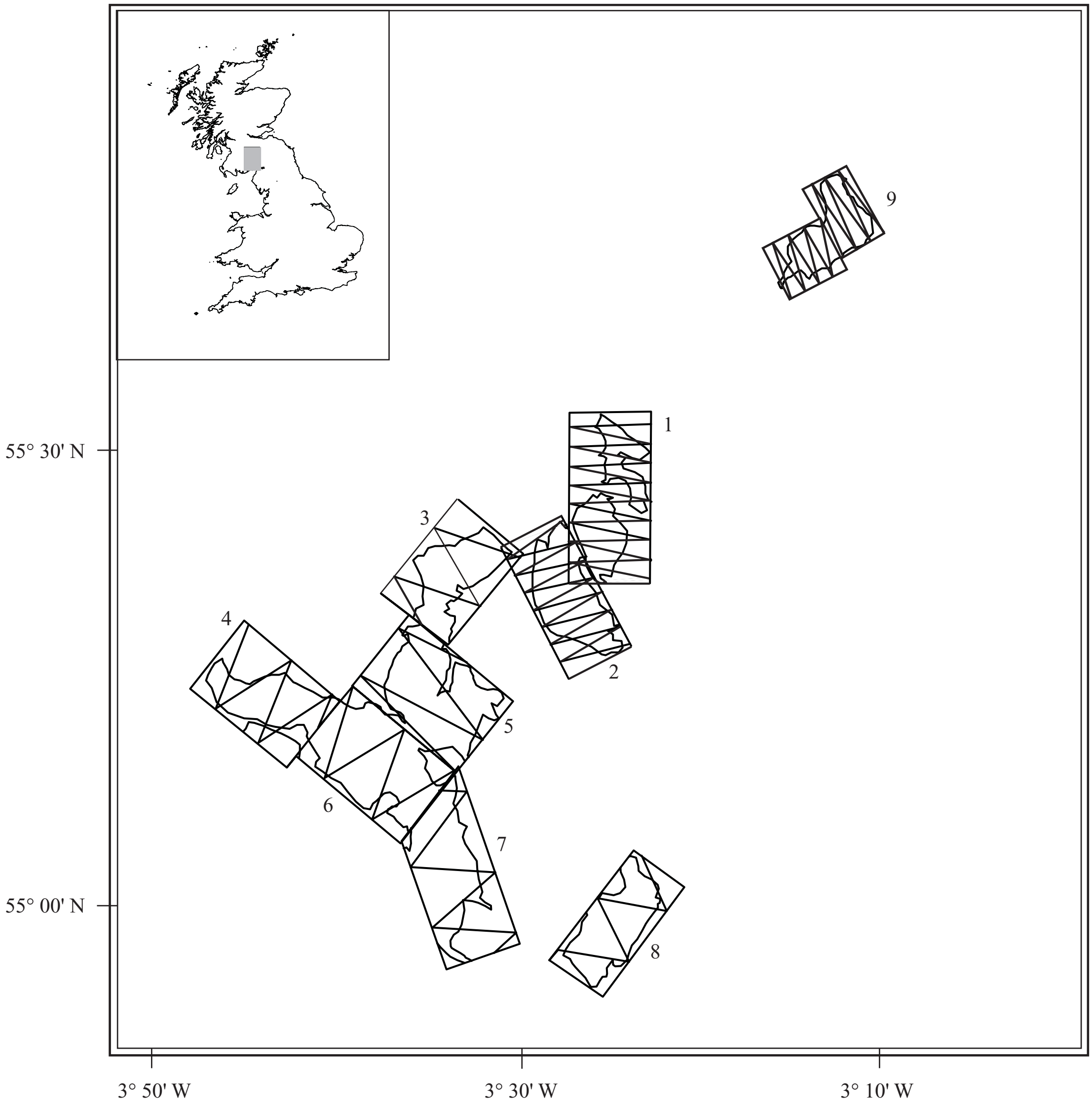

Fig. 2. Map of Tweedsmuir region showing blocks surveyed (1–9). Also shown are the orientation lines placed over the blocks following a zig-zag design, along which transects were placed. For details of the spacing between transect lines see the main text.

sika deer dung surveys in Scotland, where deer densities were relatively high, 50 m transects were found to be satisfactory. However, in areas where deer density is low, transects longer than 50 m may be more appropriate. We recommend, none the less, that there be a minimum of approximately 10–20 separate transect lines within each area of land (e.g. geographical blocks, estates, etc.) for which a separate estimate of abundance is required for effective management.

Care must be taken when choosing the timing of surveys. Seasonal environmental features, such as vegetational growth or the amount of snow cover on the ground, may lead to difficulties in finding dung. This in turn may greatly increase the level of effort required to obtain the desired precision, or may result in an underestimate of the number of animals in the region. Early December through mid-April, provided snow cover is not a problem and early spring vegetation growth has not occurred, is generally considered most practicable in Scotland.

FIELD METHODS

Once the survey design has been completed, the starting position can be determined based on topographic features extracted from a map, or by using a global positioning system (GPS). A compass can then be used to determine the direction in which observers should walk. In woodland areas, however, following a compass bearing along a straight line can be difficult. The use of a rope or cable of known length, with additional length marks along it, provides an effective means of marking the line. The cable can be placed along the desired bearing, and observers can then walk alongside it. This has the additional advantage that the transect line is clearly marked, facilitating the recording of perpendicular distances of detected objects from the line. The cable can also be used as a tool for measuring the distance that should be skipped between transect lines.

Poor quality data cannot be overcome by good data analysis. One of the most critical data collection

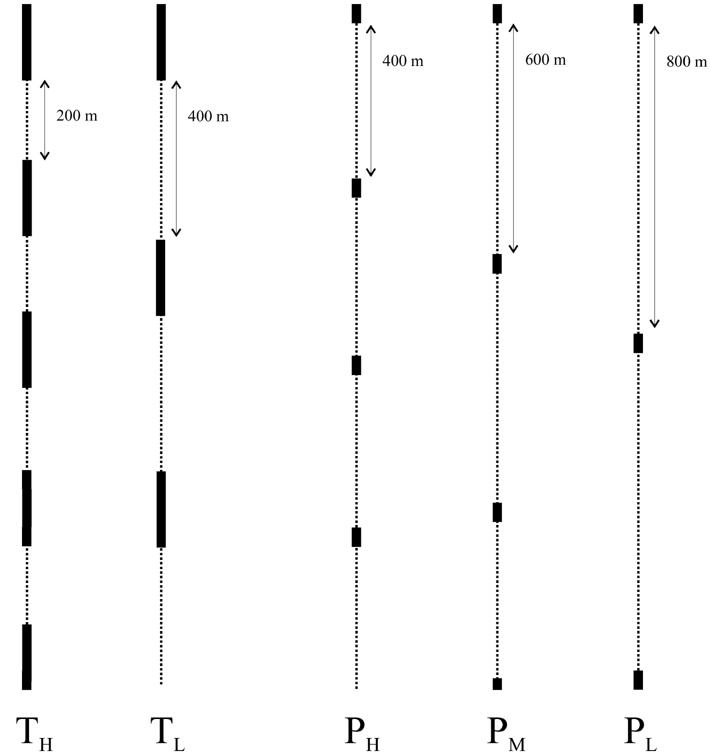

Fig. 3. Sample of gridlines (dotted lines) showing the spacing between transect lines (solid lines). For Tweedsmuir blocks, 200-m transect lines separated by 200 m and 400 m were used in high-(T_H) and low-(T_L) density blocks, respectively. For Peeblesshire blocks, 50-m transect lines separated by 400 m, 600 m and 800 m were used in high-(P_H), medium-(P_M) and low-(P_L) density blocks, respectively.

requirements is to avoid the rounding of perpendicular distance measurements, especially rounding of distances near the line to zero, as such data are difficult or impossible to model accurately. Distances should be measured from the centre of gravity of each pellet group to the line. By placing a physical line such as a rope or cable on the ground, together with a well-defined method for identifying the centre of a pellet group, the strong tendency in line transect surveys of dung to record a high proportion of detections as on the line can be avoided.

Perhaps the best way of ensuring the collection of good quality data is to have conscientious, motivated and trained observers, with a good understanding of the data collection requirements. It is also important that observers are well equipped for the conditions they will encounter, with adequate clothing, equipment and recording media.

DATA ANALYSIS

The data collected consist of the number of detected pellet groups and the perpendicular distances from the centre of each group to the transect line. Although deer density estimates by habitat type may not be of interest, stratification by habitat type will usually be required as the detection probabilities may vary according to the characteristics of the various habitats. Hence data on the habitat types associated with each transect line should also be recorded.

In the case where surveys are carried out over homogeneous habitats (e.g. all pole stage forests), the detection function can be estimated based on the full set of perpendicular distances. Encounter rate estimates can then be computed for each block (e.g. geographical area, estate, etc.), and pellet group densities by block calculated using standard line transect methods (cf. equation 2).

If habitat types vary throughout the block or area under consideration, transects should be stratified according to habitat type, and separate estimates of $f(0)$ obtained for each habitat type. Encounter rate estimates can then be obtained for each habitat type within each block, and pellet group density estimates for each habitat within a block computed according to equation 2.

To estimate deer density from pellet group density, block- and habitat-specific estimates of length of time to dung decay are required (Dzieciolowski 1976). Pellet group density estimates are then divided by estimates of the length of time to pellet group decay (i.e. the reciprocal of the decay rate) for each habitat within each block, yielding estimates of the number of pellet groups deposited per day per km^2. Deer density estimates can then be obtained by dividing these estimates by the estimated defecation rate; that is:

$$\hat{D}_{jk} = \frac{\hat{G}_{jk}}{\hat{s}} = \frac{\hat{P}_{jk}}{\hat{r}_{jk}\cdot\hat{s}} = \frac{\frac{n_{jk}}{L_{jk}}\cdot\hat{f}_{jk}(0)\cdot\frac{1}{2}}{\hat{r}_{jk}\cdot\hat{s}} \qquad \text{eqn 3}$$

where the subscripts k and j denote the habitat and block, respectively, $\hat{D}_{jk}$ is the estimated deer density for habitat k within block j, $\hat{G}_{jk}$ is the estimated number of pellet groups deposited per day per km^2, $\hat{P}_{jk}$ is the estimated pellet group density, $\hat{r}_{jk}$ is the estimate of the length of time to pellet group decay, and $\hat{s}$ is the estimate of defecation rate. Note that the defecation rate is assumed to be independent of habitat type and block. If methods are applied consistently across blocks, precision and reliability are likely to be improved by assuming $f_{jk}(0) = f_k(0)$, independent of block. Similarly, the length of time to pellet group decay might be assumed to be a function of habitat only: $r_{jk} = r_k$.

An estimate of deer abundance for each block is then obtained by multiplying the density estimate for each habitat within the block by the area covered by that habitat, and summing the resulting estimates across all q habitat types:

$$\hat{N}_j = \sum_{k=1}^{q} A_{jk} \cdot \hat{D}_{jk} = \sum_{k=1}^{q} A_{jk} \frac{\hat{P}_{jk}}{\hat{r}_{jk} \cdot \hat{s}} \qquad \text{eqn 4}$$

where $\hat{N}_j$ is the estimated deer abundance for block j, and A_{jk} indicates the area covered by habitat k within block j. If A_{jk} is not known, it can be estimated as:

$$\hat{A}_{jk} = \frac{L_{jk}}{\sum_{k=1}^{q} L_{jk}} A_j \qquad \text{eqn 5}$$

where A_j is the area of block j and L_{jk} denotes the transect length through habitat k within block j.

The sum of the abundance estimates from all blocks gives the total deer abundance in the region.

To compare deer densities in different habitat types, pellet group density for each habitat within each block is estimated as previously described, and these estimates are divided by the corresponding length of time to dung decay. The resulting estimates of the number of pellet groups deposited per day per km^2 for each habitat can then be averaged, weighted by area, across all blocks. A final estimate of deer density within a habitat type is obtained by dividing these estimates by the defecation rate. Note that, if we assume that $f(0)$ and r are functions of habitat alone, we can express average deer density for habitat k as:

$$\hat{D}_k = \frac{1}{\hat{s}} \cdot \frac{\hat{f}_k(0)}{2\hat{r}_k} \left\{ \sum_{j=1}^{m} \frac{n_{jk}}{L_{jk}} \cdot W_{jk} \right\} \qquad \text{eqn 6}$$

where $W_{jk} = A_{jk}/A_k$, specifying the proportion of the total area $A_k = \sum_{j=1}^{m} A_{jk}$ covered by habitat k that falls within block j. Factoring out terms that are common across blocks is essential for variance estimation (below).

Overall abundance is given by:

$$\hat{N} = \sum_{j=1}^{m} \hat{N}_j \qquad \text{eqn 7}$$

Note that this can be expressed as:

$$\hat{N} = \sum_{k=1}^{q} A_k \hat{D}_k \qquad \text{eqn 8}$$

a result that is useful for valid variance estimation when some parameters are common across blocks, as in equation 6.

ESTIMATION OF LENGTH OF TIME TO DUNG DECAY AND DEER DEFECATION RATES

Dung decay refers to the disappearance of pellet groups irrespective of the mechanism by which the process occurred. For example, pellet groups that have been covered by leaves, that have been spread out over a large area as a result of trampling by the deer, or that have undergone organic decay, all are considered as decayed as long as they are no longer recognizable as a pellet group. Ideally, the length of time to dung decay should be monitored by locating a random, or at least representative, sample of fresh pellet groups from throughout the study area. We require the length of time to decay for pellets deposited in the months preceding the line transect survey. A possible design is to locate samples of fresh dung monthly, for a period close to the maximum likely duration of the most durable pellets. The proportion of pellets surviving to the time of the line transect survey should then be recorded, and this proportion can be modelled parametrically as a function of date, from which mean time to decay can be estimated. In practice, it is difficult to meet this ideal, and there are many potential sources of bias. If fresh dung from elsewhere is positioned at random locations, these locations may prove unrepresentative of where the deer defecate. Also, the monitoring of pellet groups until they disappear will give an estimate of the life span of freshly deposited pellet groups, rather than an estimate of the average life span of pellet groups that were on the ground at the time of the survey.

A number of studies have shown that daily defecation rates vary seasonally and are influenced by habitat quality and sex/age class differences in feeding behaviour (Van Etten & Bennett 1965; Neff 1968; Dzieciolowski 1976; Mitchell *et al.* 1985; Mayle *et al.* 1996). Ideally defecation rates should be estimated for the population under consideration. However, this is generally not practical and so defecation rates are estimated for captive animals in a 'natural' habitat on as 'natural' (minimum supplementary feed) a diet as possible. In practice, bias from this source is likely to be less problematic than bias in estimates of decay length.

VARIANCE ESTIMATION

Estimation of $\text{var}\{\hat{f}_{jk}(0)\}$ and $\text{var}(n_{jk})$ is described by Buckland *et al.* (1993), and is most easily done using the software DISTANCE (Laake *et al.* 1993). The variance of the abundance estimates for each block is derived using the delta method (pp. 7–9 in Seber 1982; p. 53 in Buckland *et al.* 1993). If no parameters other than defecation rate are assumed to be common across habitats and blocks, we have:

$$\widehat{\text{var}}(\hat{N}_j) = \hat{N}_j^2 \left\{ \frac{\widehat{\text{var}}(\hat{s})}{\hat{s}^2} + \frac{\sum_{k=1}^{q} A_{jk}^2 \widehat{\text{var}}(\hat{G}_{jk})}{(\sum_{k=1}^{q} A_{jk} \hat{G}_{jk})^2} \right\} \qquad \text{eqn 9}$$

where:

$$\widehat{\mathrm{var}}(\hat{G}_{jk}) = \hat{G}_{jk}^2\left\{\frac{\widehat{\mathrm{var}}(n_{jk})}{n_{jk}^2} + \frac{\widehat{\mathrm{var}}\{\hat{f}_{jk}(0)\}}{\{\hat{f}_{jk}(0)\}^2} + \frac{\widehat{\mathrm{var}}(\hat{r}_{jk})}{\hat{r}_{jk}^2}\right\} \quad \text{eqn 10}$$

Approximate 95% log-normal confidence intervals for the abundance estimates for each block can then be computed as described in Buckland *et al.* (1993).

The precision of density estimates for each habitat can be estimated as (Buckland *et al.* 1993):

$$\widehat{\mathrm{var}}(\hat{D}_k) = \hat{D}_k^2\left\{\frac{\widehat{\mathrm{var}}(\hat{s})}{\hat{s}^2} + \frac{\sum_{j=1}^m W_{jk}^2\widehat{\mathrm{var}}(\hat{G}_{jk})}{(\sum_{j=1}^m W_{jk}\hat{G}_{jk})^2}\right\} \quad \text{eqn 11}$$

If $f_k(0)$ and length of time to pellet group decay r_k are assumed to vary by habitat k but not by block, the equation for $\widehat{\mathrm{var}}(\hat{N})$ remains the same, but we now have:

$$\widehat{\mathrm{var}}(\hat{D}_k) = \hat{D}_k^2\left\{\frac{\widehat{\mathrm{var}}(\hat{s})}{\hat{s}^2} + \frac{\widehat{\mathrm{var}}\{\hat{f}_k(0)\}}{\{\hat{f}_k(0)\}^2} + \frac{\widehat{\mathrm{var}}(\hat{r}_k)}{\hat{r}_k^2} + \frac{\sum_{j=1}^m \widehat{\mathrm{var}}\{\hat{M}_{jk}\}}{\{\sum_{j=1}^m \hat{M}_{jk}\}^2}\right\} \quad \text{eqn 12}$$

where:

$$\hat{M}_{jk} = \frac{n_{jk}}{L_{jk}} \cdot W_{jk} \quad \text{eqn 13}$$

and:

$$\widehat{\mathrm{var}}(\hat{M}_{jk}) = \frac{W_{jk}^2}{L_{jk}^2}\widehat{\mathrm{var}}(n_{jk}) \quad \text{eqn 14}$$

The variance of the total estimate of deer abundance can be obtained as:

$$\widehat{\mathrm{var}}(\hat{N}) = \widehat{\mathrm{var}}\left(\sum_{k=1}^q \hat{D}_k A_k\right) = \sum_{k=1}^q A_k^2\widehat{\mathrm{var}}(\hat{D}_k) \quad \text{eqn 15}$$

using the appropriate expression for $\widehat{\mathrm{var}}(\hat{D}_k)$. Ninety-five per cent log-normal confidence intervals are then computed as described in Buckland *et al.* (1993).

For more complex designs, for example when some decay lengths are common across different habitats and $f(0)$ estimates are common across blocks for a given habitat, variance estimates may be found by bootstrapping (Efron & Tibshirani 1993). To generate a bootstrap sample, first resample with replacement transects within each block until the total transect length is again L_j. Next simulate a bootstrapped length of time to pellet group decay for each habitat/block combination for which decay lengths are assumed to differ. If we have an estimate $\hat{r}$ with variance $\widehat{\mathrm{var}}(\hat{r})$, we can achieve this by simulating a value from a normal distribution $\mathcal{N}(\hat{r},\widehat{\mathrm{var}}(\hat{r}))$. Next simulate a defecation rate from $\mathcal{N}(\hat{s},\widehat{\mathrm{var}}(\hat{s}))$. Now analyse the bootstrap sample as if it was the original sample. Repeat this procedure for a large number of resamples, and estimate variances and intervals using standard bootstrap methods (Efron & Tibshirani 1993). One advantage of this approach is that it incorporates the uncertainty arising from estimating A_{jk} from equation 5.

Example: sika deer abundance in south Scotland

As an example we applied the methodology outlined above to estimate sika deer abundance in south Scotland. Sika deer were introduced in Scotland at the beginning of the century, and information from culls and sightings (Deer Commission for Scotland, unpublished data) suggests that the population is increasing. As with other deer species, sika deer can cause damage to forest plantations and woodland habitats. In addition, sika deer hybridize with red deer in areas where the two species overlap, and there is evidence that introgression of the red deer genotype is taking place at these hybridization zones (Abernethy 1994). Hence there is a need to devise a management plan for the species, and accurate and precise estimates of sika deer abundance are required. Because sika deer spend most of their time in woodland areas, abundance estimates are based on pellet group counts. We applied line transect methods to estimate sika deer pellet group density by geographical block and habitat type, based on surveys conducted in the Tweedsmuir (Fig. 2) and Peeblesshire (Fig. 1) regions of south Scotland. Survey design and data analysis differed between regions, and therefore they are described separately.

TWEEDSMUIR REGION

Study area and survey design

The survey area in the Tweedsmuir region was divided into nine geographical blocks (Fig. 2), with greater survey effort being allocated to blocks thought to contain higher deer densities (blocks 1 and 2) based on cull and sightings data (Deer Commission for Scotland, unpublished data). After choosing a random starting point within each block, transect lines were placed in a zig-zag fashion across each block. To improve the spatial coverage in higher density blocks, transect lines were placed 200 m apart so that, for each 200-m segment surveyed, the following 200 m were skipped, then the next 200 m surveyed, and so on (Fig. 3). The position of transect lines within lower density blocks was determined as described above, but only every third 200-m segment was surveyed. This resulted in approximately two and five transect lines per km^2 in low- and high-density blocks, respectively.

Surveys of sika deer dung were carried out by the Deer Commission for Scotland from March through May of 1997. Observers walked along transect lines recording the perpendicular distance from the centre of each detected pellet group to the transect line. Only pellet groups containing 16 or more pellets were counted. The value of 16 was chosen to reduce the risk of counting a widely spread pellet group as two groups, which would lead to overestimation of density. Pellet groups whose centres were located further than 2 m from the transect line were not counted. Each 200-m transect was divided into 50-m segments, and the predominant habitat type (open ground, prethicket, thicket, pole stage or pole stage thinned) within each segment was recorded.

Data analysis

In order to model the detection function of the perpendicular distances from the Tweedsmuir blocks, data were pooled across all blocks and transect lines stratified according to habitat type. Separate estimates of $f(0)$ were then obtained for each habitat using the program DISTANCE (Laake *et al.* 1993). Three models for the detection function were considered: half-normal, uniform and hazard rate. In each case the need for cosine adjustment terms was assessed using likelihood ratio tests. Choice of the final model was based on a combination of a low Akaike's information criterion (AIC) and a low variance. Initially data from block 9 were to be analysed separately as no prior information on deer densities was available for that block. However, due to the small sample size, estimates of $f(0)$ for block 9 were obtained by pooling data from that block and the remaining Tweedsmuir blocks, and repeating the analysis as described above. Encounter rate was estimated separately for each habitat within each block, and its variance computed empirically (Buckland *et al.* 1993). Having estimated $f(0)$ and encounter rate (n/L) for all strata, pellet group density for each habitat within each block was computed according to equation 2.

Decay length estimates were obtained by monitoring fresh pellet groups within a given habitat between August 1995 and April 1996, and recording the length of time (days) to decay (< 6 pellets remaining). Results from earlier work (B.A. Mayle & A.J. Peace, unpublished data) indicated that the average time for a pellet group to decay was a function of the initial pellet group size, the final pellet group size, and individual pellet decay rates. For each habitat the average length of time to pellet group decay was modelled using a method similar to Plumptre & Harris (1995), modified to ascertain what decay lengths should be used when assessing dung in any given month. Unfortunately, estimates of the length of time to dung decay were not site specific and were only available for pooled habitat types (cf. Table 1). Therefore, for each block, density estimates from the prethicket and thicket habitats and from the pole stage and pole stage thinned habitats were averaged, weighted by the effort expended within each habitat. These pooled estimates plus the density estimate for the open ground habitat were then divided by the estimated length of time to dung decay for each habitat group corresponding to the month in which the block was surveyed (Table 1), yielding estimates of the number of pellet groups deposited per day per km^2. Deer density estimates were then obtained by dividing these estimates by the defecation rate of 25 pellet groups per day (Mayle & Staines 1998). A final density estimate for the block was computed as an effort-weighted average of densities from the three habitat groups. We used effort as weights in the analysis because data on the area covered by each habitat type were not available. However, as transect lines were randomly placed across the blocks, the effort expended within each habitat type should, on average, be proportional to the area covered by each habitat. Equivalently, the area covered by each habitat could be estimated according to equation 5. Deer abundance for the block was obtained by multiplying the final density estimate by the block area. Abundance estimates from all blocks were summed, yielding an estimate of total deer abundance. Sika deer densities by habitat type were computed as described in Methodology, except that estimates of length of time to pellet group decay varied across blocks (because they were not all surveyed in the same month), and so r_k was removed from equation 6 and the term inside the summation was divided by the corresponding estimate of length of time to pellet group decay r_{jk}.

The precision of the abundance estimates for each block could not be computed as described in equations 9–10 because estimates of the length of time to pellet group decay were common to more than one habitat within a given block. Estimates of decay length also differed by month, and hence by block. Thus we estimated the variance of the estimated deer density for each habitat within each block as:

$$\widehat{\text{var}}(\hat{D}_{jk}) = \hat{D}_{jk}^2 \left\{ \frac{\widehat{\text{var}}(n_{jk})}{n_{jk}^2} + \frac{\widehat{\text{var}}\{\hat{f}_k(0)\}}{\{\hat{f}_k(0)\}^2} + \frac{\widehat{\text{var}}(\hat{r}_{jk})}{\hat{r}_{jk}^2} \right\} \quad \text{eqn 16}$$

and computed the overall precision of the density estimate for the block as the variance of the effort-weighted average of the individual variances:

$$\widehat{\text{var}}(\hat{D}_j) = \widehat{\text{var}}\left(\sum_{k=1}^{q} \hat{D}_{jk} \cdot \frac{L_{jk}}{\sum_{k=1}^{q} L_{jk}} \right) = \sum_{k=1}^{q} \left\{ \frac{L_{jk}}{\sum_{k=1}^{q} L_{jk}} \right\}^2 \widehat{\text{var}}(\hat{D}_{jk}) \quad \text{eqn 17}$$

As there are no available estimates for the variance of sika deer defecation rate estimates ($\hat{s}$), it was assumed to be zero. Although this will underestimate the overall variance, in practice the contribution of the defecation rate estimate to the variance will be small, unless its coefficient of variation (CV) approaches the magnitude

Table 1. Estimates of dung decay rates (in days) and their standard error (SE) for habitat groups, by month. Note that SE is assumed constant across months. Tweedsmuir block 1 was surveyed in March, blocks 2–7 in April, and blocks 8–9 in May 1997. Peeblesshire blocks 14 and 17–34 were surveyed in February, blocks 1–9, 11, 13, 15–16 in March, and blocks 10 and 12 in April 1998

Habitat group	February	March	April	May	SE
Open ground	137	151	163	174	13
Prethicket + thicket	155	161	169	177	14
Pole stage + pole stage thinned	324	314	300	287	28

of the CV for encounter rate. Because the defecation rate required is an average across animals, and across the months preceding the line transect survey, uncertainty in its estimation would have to be large indeed to match the uncertainty in estimating encounter rate. Approximate 95% log-normal confidence intervals for the abundance estimates for each block were then computed as described in Buckland *et al.* (1993). The precision of the total abundance estimate could not be obtained using analytical methods because $\hat{f}(0)$ and decay length estimates common to more than one block could not be factored out. Instead we used the bootstrap procedure to obtain 95% 'percentile' confidence intervals (Efron & Tibshirani 1993) for the total abundance estimate.

The precision of density estimates by habitat type was estimated as in equation 12, except that estimates of the length of time to pellet group decay varied by block. Therefore the last two terms in equation 12 were replaced by $\sum_{l=1}^{v} \widehat{\text{var}}(\hat{Q}_{lk}) / (\sum_{l=1}^{v} \hat{Q}_{lk})^2$, where:

$$\hat{Q}_{lk} = \frac{1}{\hat{r}_{lk}} \cdot \sum_{j \in R_l} \hat{M}_{jk} \qquad \text{eqn 18}$$

$$\widehat{\text{var}}(\hat{Q}_{lk}) = \hat{Q}_{lk}^2 \left\{ \frac{\widehat{\text{var}}(\hat{r}_{lk})}{\hat{r}_{lk}^2} + \frac{\sum_{j \in R_l} \widehat{\text{var}}(\hat{M}_{jk})}{(\sum_{j \in R_l} \hat{M}_{jk})^2} \right\} \qquad \text{eqn 19}$$

and R_l $(l = 1, \ldots, v)$ denotes the set of blocks containing a common estimate of the length of time to pellet group decay $\hat{r}_{lk}$. The variance of the defecation rate estimate was taken to be zero. Data from block 9 were not included in this analysis to simplify the computation of the variance. Ninety-five per cent log-normal confidence intervals were computed as described in Buckland *et al.* (1993).

Results

Examination of the perpendicular distance data stratified by habitat type did not indicate any apparent rounding problems (Fig. 4). Table 2 shows estimates

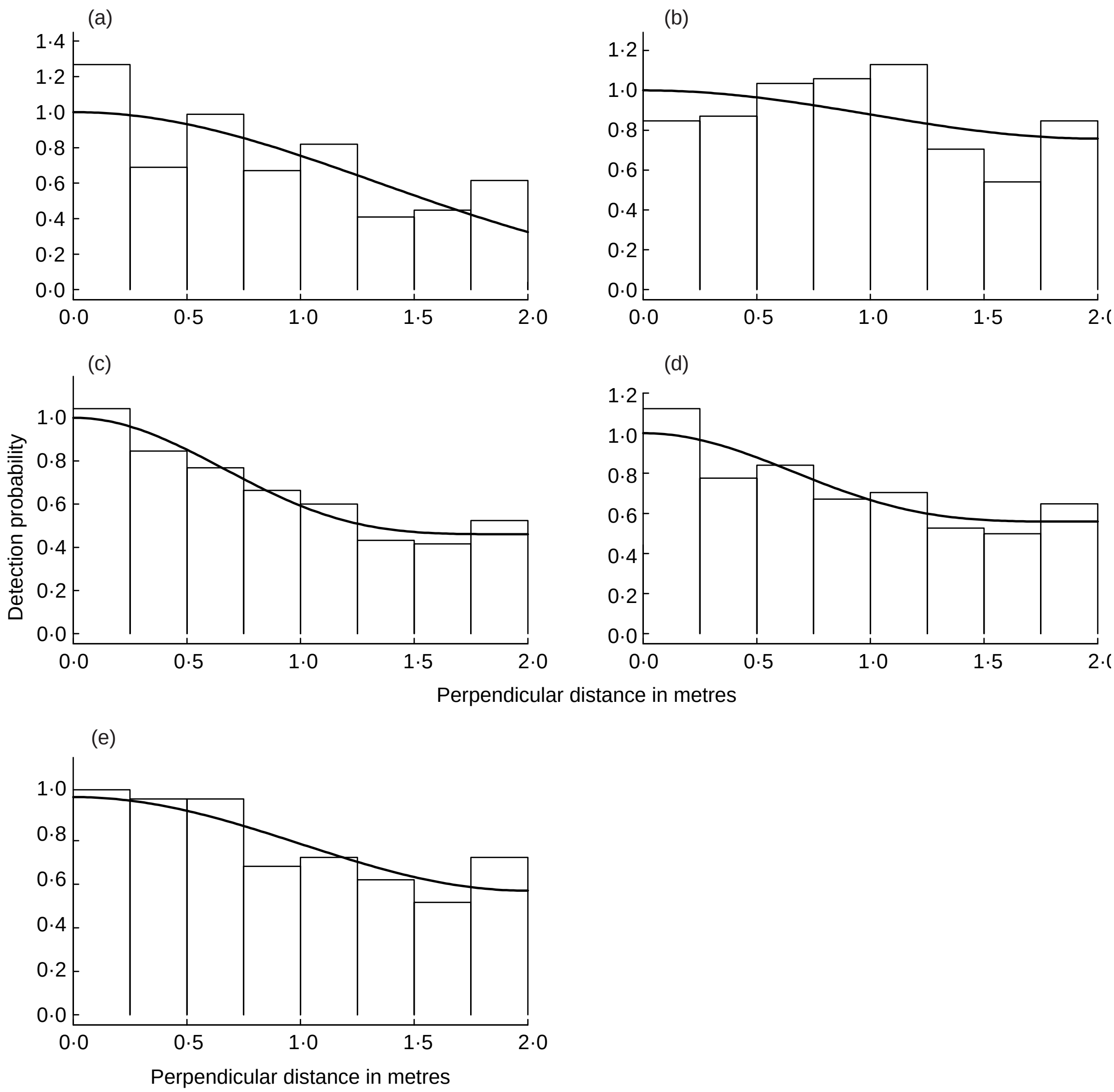

Fig. 4. Histograms of perpendicular distances and fitted detection functions for (a) open ground, (b) prethicket, (c) thicket, (d) pole stage and (e) pole stage thinned habitats within Tweedsmuir blocks, except block 9.

Table 2. Estimates of $f(0)$ (in m^{-1}), corresponding SE and percentage coefficient of variation (% CV) for habitats within all Tweedsmuir blocks except block 9, within all Tweedsmuir blocks, and within Peeblesshire blocks. Open ground (a) refers to open ground habitat within forested areas, and open ground (b) to open ground areas between 0 m and 300 m from the forest edge

Region	Habitat	Model	$f(0)$	$\widehat{SE}\{f(0)\}$	% CV
Tweedsmuir					
(excluding	Open ground	Half-normal + 1 cos adj.	0·6750	0·0354	5·25
Block 9)	Prethicket	Uniform + 1 cos adj.	0·5689	0·0408	7·18
	Thicket	Uniform + 2 cos adj.	0·7557	0·0246	3·26
	Pole stage	Uniform + 2 cos adj.	0·6914	0·0283	4·09
	Pole stage thinned	Uniform + 1 cos adj.	0·6369	0·0397	6·23
Tweedsmuir					
(including	Open ground	Half-normal	0·6913	0·0341	4·93
Block 9)	Prethicket	Uniform + 1 cos adj.	0·6452	0·0325	5·04
	Thicket	Uniform + 2 cos adj.	0·7636	0·0230	3·01
	Pole stage	Uniform + 2 cos adj.	0·6986	0·0274	3·93
	Pole stage thinned	Uniform + 2 cos adj.	0·7303	0·0541	7·41
Peeblesshire					
	Open ground (a)	Half-normal	0·5033	0·0324	6·45
	Open ground (b)	Uniform + 1 cos adj.	0·9431	0·1579	16·75
	Prethicket	Uniform + 1 cos adj.	0·6022	0·0217	3·60
	Thicket	Half-normal + 1 cos adj.	0·7093	0·0555	7·82
	Pole stage	Uniform	0·5076	0·0000	0·00
	Pole stage thinned	Uniform	0·5000	0·0000	0·00

Table 3. Estimates of sika deer abundance ($\hat{N}$) and density ($\hat{D}$) with 95% confidence intervals (CI) and percentage coefficient of variation (%CV) for Tweedsmuir blocks

Block	$\hat{N}$	95% CI for $\hat{N}$	$\hat{D}$	95% CI for $\hat{D}$	%CV
1	292	240–356	20·94	17·21–25·49	10·04
2	50	37–66	4·84	3·63–6·44	14·67
3	12	8–17	1·40	0·94–2·07	20·39
4	11	7–17	1·38	0·86–2·20	24·25
5	22	8–64	1·57	0·55–4·48	57·62
6	32	20–52	2·10	1·29–3·43	25·29
7	14	9–22	1·24	0·77–2·00	24·47
8	16	10–24	1·66	1·07–2·58	22·64
9	21	17–27	3·59	2·85–4·53	11·91
Total	470	406–573			9·37

of $f(0)$ for each habitat within all Tweedsmuir blocks except block 9, and within all Tweedsmuir blocks combined.

Estimates of the number of deer per km^2 in block 1 far exceeded density estimates from all other blocks (Table 3). Point estimates of density in blocks 2 and 9 were slightly greater than those from the remaining blocks, with fairly narrow confidence intervals. However, the precision of density estimates for the remaining blocks was generally poor, and their confidence intervals often overlapped those from blocks 2 and 9 (see estimates for blocks 5 and 6). A total of 470 deer was estimated for the region. We used the CV, $CV(\hat{D}) = \sqrt{\widehat{\text{var}}(\hat{D})}/\hat{D}$, as a measure of precision.

Estimates of sika deer density by habitat type (Table 4) indicated higher densities in thicket habitat, followed by prethicket and open ground areas.

Table 4. Estimates of sika deer density ($\hat{D}$), 95% confidence intervals (CI) and percentage coefficient of variation (% CV) by habitat type within Tweedsmuir blocks, forested areas within all Peeblesshire blocks [Peeblesshire (a)], and open ground areas within forested area [Peeblesshire (b)] and within 0–300 m from the forest [Peeblesshire (c)] for Peeblesshire blocks 9–13 and 15–16

Location	Habitat	$\hat{D}$	95% CI	% CV
Tweedsmuir				
	Open ground	9·10	8·10–10·23	5·97
	Prethicket	9·73	8·15–11·61	9·06
	Thicket	14·88	13·65–16·22	4·40
	Pole stage	4·42	3·97–4·91	5·39
	Pole stage thinned	1·67	1·40–1·99	9·00
Peeblesshire (a)				
	Open ground	14·66	10·53–20·42	17·01
	Prethicket	48·59	37·72–62·59	12·98
	Thicket	19·56	14·66–26·11	14·81
	Pole stage	2·64	1·60–4·34	25·82
	Pole stage thinned	2·35	1·50–3·67	23·10
Peeblesshire (b)				
	Open ground	20·62	8·46–50·23	47·88
Peeblesshire (c)				
	Open ground	2·94	1·22–7·08	47·07

PEEBLESSHIRE REGION

Study area and survey design

Surveys in the Peeblesshire region (Fig. 1) were carried out from February through April of 1998. The survey area was divided into 33 geographical blocks, and three levels of survey effort were allocated to groups of blocks thought to contain high (blocks 1–16), medium (blocks 22, 26–27) and low (blocks 17–21, 23–25, 28–33) deer densities based on cull and sightings data (Deer Commission for Scotland, unpublished data). Given the results from surveys conducted in the Tweedsmuir region and the expected densities in Peeblesshire, transect lengths were reduced in order to increase the number of transects surveyed, and thus improve estimation of precision of abundance estimates. Fifty-metre transects were placed following a north–south grid of lines, with the distance between lines being equal to the distance between transects along the lines. The spacing between lines (400 m, 600 m and 800 m for high-, medium- and low-density blocks, respectively; cf. Fig. 3) was determined to maximize the spatial coverage given the available effort, resulting in a sampling intensity of approximately two, four and seven transect lines per km^2 for low-, medium- and high-density blocks, respectively. To quantify the extent of the usage of open ground areas by sika deer, additional 50-m transects were placed along the grid of lines up to 300 m beyond the edge of the forest in some of the high-density blocks (blocks 9–13 and 15–16). The original spacing between transect lines (400 m) was followed, but only every fifth transect was surveyed.

Line transect surveys were conducted as described for the Tweedsmuir region, except that this time the predominant habitat type was recorded for every 10-m segment within a 50-m transect line.

Data analysis

Estimation of deer density for each habitat within each block was carried out as for the Tweedsmuir region. For the high-density blocks, separate analyses were carried out for forested (A) and open ground areas between 0 and 300 m from the forest edge (B), with separate estimates of f(0) and encounter rate obtained for each of these two groups. Abundance estimates for each block, and also for each of the two groups described above, were obtained according to equation 4. The area covered by each habitat within each block was estimated according to equation 5. Total abundance estimates for blocks 9–13, 15 and 16 were obtained by summing abundance estimates from forested (A) and open ground (B) areas within each block.

Sika deer density estimates by habitat type were obtained as described for the Tweedsmuir region, with the area covered by each habitat type within each block being estimated according to equation 5, and the total area covered by a given habitat in all blocks estimated as:

$$\hat{A}_k = \sum_{j=1}^{m} \hat{A}_{jk} = \sum_{j=1}^{m} \left\{ \frac{L_{jk}}{\sum_{k=1}^{q} L_{jk}} A_j \right\} \quad \text{eqn 20}$$

so that the weights used became:

$$W_{jk} = \frac{\hat{A}_{jk}}{\hat{A}_k} \quad \text{eqn 21}$$

An estimate of the overall sika deer abundance in the region was obtained by summing the abundance estimates from all low- and medium-density blocks, and also from the two groups (A, B) within blocks 9–13, 15–16.

Precision of the abundance estimates for each block was computed as described for the Tweedsmuir region. The bootstrap was used to estimate the precision of the total abundance estimate for the region, with data from each of the two groups (A, B) being analysed separately. For group A, bootstrap estimates of abundance were substantially lower on average than the original estimate. This occurred because several blocks contained very little habitat preferred by deer, with just one transect segment falling within the high-density habitats. For bootstrap resamples in which this segment was not selected, there would be no effort in that habitat, resulting in an abundance estimate of zero. This underestimation was not offset by resamples in which the segment was selected more than once; for example, if it was selected twice, both the effort and the sample size for that habitat would be doubled, but encounter rate and the estimated density would remain unaltered. For group A the problem was particularly acute because of the confluence of three factors: a large number of relatively small blocks; small quantities of prethicket and thicket habitat in many blocks; and deer densities an order of magnitude higher in prethicket and thicket habitats relative to pole stage forest. The practical effect on the analysis was to lead to bootstrap estimates whose mean and variance were both biased low. However, the bootstrap CV was likely to be estimated relatively reliably, and so we used this CV to obtain the variance for the total abundance from blocks within group A. Due to the small sample size it was not possible to bootstrap data from transects between 0 and 300 m from the forest edge. Instead we computed an approximate variance for that group analytically, and added this variance to the estimated bootstrap variance for the other group. Ninety-five per cent confidence intervals were then computed based on the total variance.

Results

Histograms of the perpendicular distance data from forested areas within Peeblesshire are presented in Fig. 5, stratified by habitat type.

Deer density estimates indicated generally higher densities for blocks within forested areas than in areas beyond the forest edge (Table 5). Precision for both groups was poor for blocks containing small sample sizes and for those with large variability in encounter rate between lines. As anticipated, blocks 1–16 had higher deer densities. No pellets were observed in nine of the 33 blocks surveyed, resulting in zero density and abundance estimates for these blocks. Note that some of the high-density blocks had low estimates of abundance due to their small area. A total of 620 deer was estimated to be present in the region.

As in the Tweedsmuir blocks, sika deer density estimates by habitat type indicated higher densities in prethicket and thicket areas (Table 4). Density in open

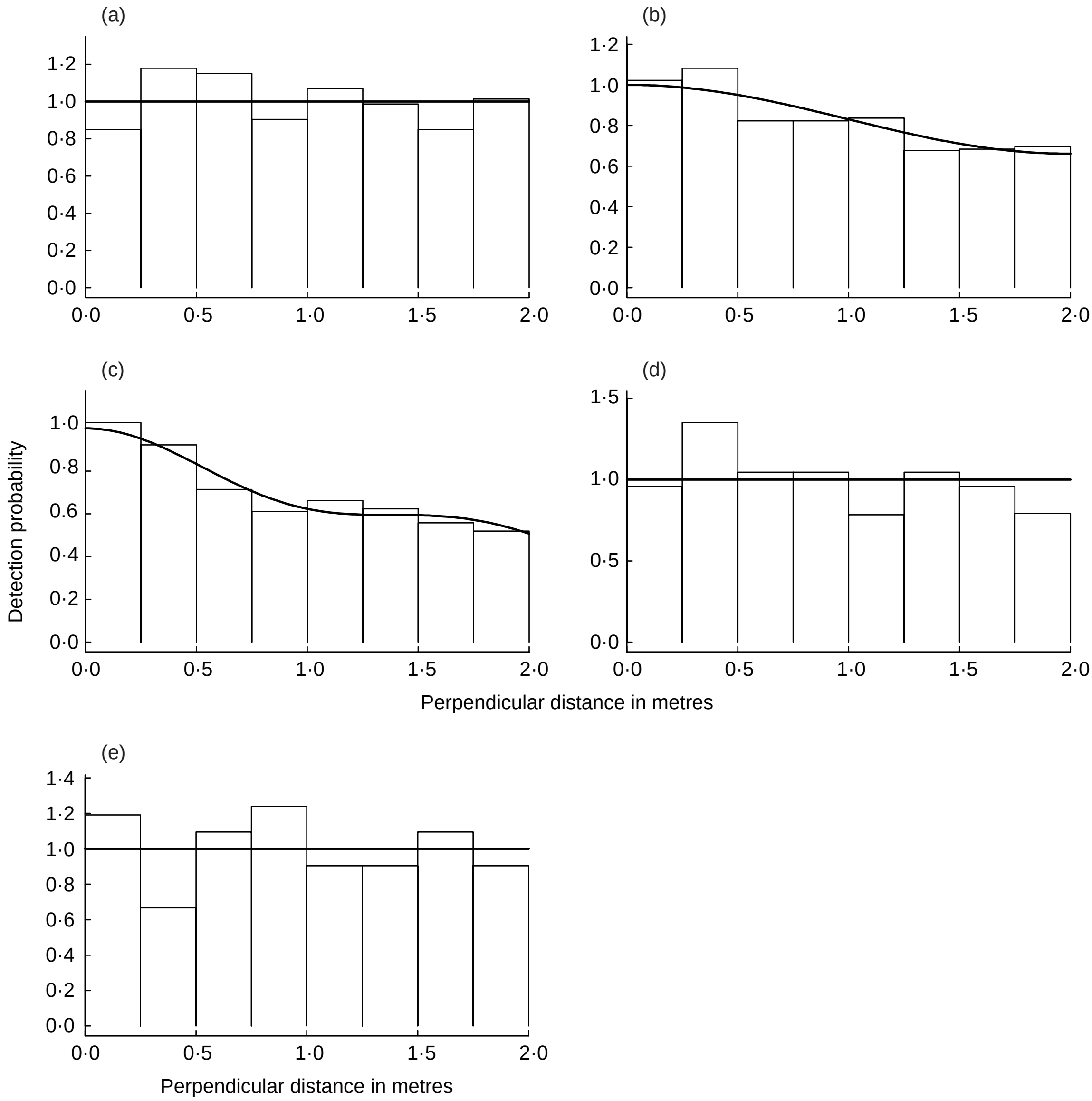

Fig. 5. Histograms of perpendicular distances and fitted detection functions for (a) open ground, (b) prethicket, (c) thicket, (d) pole stage and (e) pole stage thinned habitats within Peeblesshire forest blocks.

ground areas within the forest (which included heavily used parkland on block 12) was 10 times greater than that beyond the forest edge.

Discussion

Deer densities estimated from pellet group counts reflect average density over the time period corresponding to decay length (Buckland 1992). Hence density estimates by habitat type indicate habitat use and preferences by the animals. High sika deer densities observed in prethicket and thicket habitats within forested areas conform with findings from elsewhere in Scotland (Chadwick, Ratcliffe & Abernethy 1996). Note that deer densities by habitat type (Table 4) appear high in comparison with those obtained by block (Tables 3 and 5) because most blocks comprised predominantly low-density habitats.

Relatively high deer densities were also found in open ground areas up to 300 m from the forest edge, probably due to animals feeding on open ground at the forest edge. Although these densities were lower than the corresponding densities within the forest, the total forest edge area is large and the resulting deer abundance estimates for this region represented 27% of the combined abundance from forested and open ground areas for blocks 9–13, 15 and 16. Thus the non-inclusion of forest edge areas in deer surveys may result in an underestimate of the true deer abundance in the region. As surveys within the Tweedsmuir region did not encompass open ground areas in the vicinity of the forest edge, the total estimated abundance of around 470 animals for that region should be viewed as a minimum figure.

The most recent estimate of sika deer abundance in south Scotland gives a total of between 500 and 600 animals in 1990 (Chadwick, Ratcliffe & Abernethy

Table 5. Estimates of sika deer abundance ($\hat{N}$) and density ($\hat{D}$) with 95% confidence intervals (CI) and percentage coefficient of variation (%CV) for Peeblesshire blocks. Also shown are results from surveys conducted (a) within forested areas, and (b) between 0 m and 300 m from the forest edge for blocks 9–13, 15 and 16

Block	$\hat{N}$	95% CI for $\hat{N}$	$\hat{D}$	95% CI for $\hat{D}$	% CV
1	70	46–107	28·60	18·75–43·65	21·81
2	22	16–31	5·36	3·79–7·58	17·85
3	2	1–6	1·70	0·55–5·23	62·44
4	2	0–9	0·85	0·19–3·86	89·93
5	1	0–2	6·28	3·07–12·82	37·68
6	1	0–4	0·72	0·20–2·54	71·52
7	6	2–19	3·04	0·98–9·42	62·88
8	184	140–243	44·19	33·53–58·25	14·16
9a	66	35–125	16·10	8·49–30·54	33·55
9b	26	6–119	3·21	1·71–14·48	89·72
10a	0	–	0	–	–
10b	0	–	0	–	–
11a	3	1–6	2·23	1·06–4·69	39·35
11b	0	–	0	–	–
12a	31	14–69	19·06	8·51–42·70	42·96
12b	3	1–14	0·77	0·15–4·02	101·71
13a	22	14–35	16·85	10·58–26·82	24·06
13b	5	1–27	2·50	0·48–13·04	101·76
14	5	1–21	2·39	0·57–9·94	83·55
15a	17	6–46	7·41	2·74–20·02	54·17
15b	14	5–38	9·99	3·74–26·68	53·43
16a	37	23–60	12·76	7·85–20·73	25·16
16b	16	3–85	5·00	0·96–26·08	101·76
17	0	–	0	–	–
18	1	0–5	0·11	0·02–0·49	90·23
19	0	–	0	–	–
20	0	–	0	–	–
21	0	–	0	–	–
22	47	31–71	4·91	3·24–7·43	21·40
23	12	3–47	1·63	0·42–6·39	78·89
24	12	4–32	2·22	0·83–5·94	53·48
25	1	0–3	0·13	0·04–0·38	61·09
26	1	0–5	0·08	0·02–0·40	96·42
27	5	2–12	0·20	0·08–0·47	46·64
28	0	–	0	–	–
29	0	–	0	–	–
30	0	–	0	–	–
31	4	2–9	0·51	0·23–1·14	42·30
32	0	–	0	–	–
33	4	2–10	0·31	0·12–0·76	48·70
Total	620	507–758			10·30

1996). Our combined total from the Tweedsmuir and Peeblesshire regions is of the order of 1100 deer within the surveyed regions of south Scotland [point estimate of 1078 after allowing for the fact that Tweedsmuir's block 9 (Peeblesshire's block 23) was surveyed in both years; 95% confidence interval (938, 1239)]. Sika deer from south Scotland are among the most fertile in Scotland (Chadwick, Ratcliffe & Abernethy 1996), and they continue to expand their range (Rose 1994). An increase in cull levels in the Tweedsmuir area has been implemented successfully (Deer Commission for Scotland, unpublished data). However, continued monitoring of the population is required to determine the rate of increase and patterns of spread of the south Scotland sika deer population.

One potential source of bias when applying line transect methods arises from sampling in hilly areas. When converting estimated density of animals to abundance estimates, we assume that the transects lie on flat ground. If transects fall on slopes, the effective transect lengths will be smaller than the transect lengths actually surveyed, resulting in an underestimate of encounter rate. To estimate the bias arising from this assumption, the slope of each transect line within the Peeblesshire region was estimated, and the projected horizontal length of each 50-m transect calculated. The bias in line lengths was found to be of the order of 0·23% for these surveys. To account for this bias, the total abundance estimates for the Peeblesshire blocks presented in this paper should be increased by 0·23% (i.e. the total of 620 animals should be increased by two animals). Given the small size of this correction, it does not seem necessary to revise the method to allow for this source of bias. However, in areas of steep terrain, adjustment for this source of bias should be considered.

Another potential source of bias in the abundance estimates presented in this paper results from the use of decay length estimates that were not site specific and that had been obtained in previous years. Dung decay rates are known to vary as a function of large- and small-scale environmental conditions (e.g. Van Etten & Bennett 1965). However, modelling of the variability in decay rate estimates in both space and time is needed before the magnitude of this bias can be assessed.

The dung survey work described in this paper was carried out independently from the study of pellet group decay lengths, and there was a discrepancy in the definition of what constitutes a 'decayed' pellet group. For the line transect surveys, pellet groups containing material judged to correspond to less than 16 pellets were considered 'decayed' and thus were not counted. For the estimation of decay lengths, however, 'decayed' groups were defined to be those containing less than six individually identifiable pellets. This will bias the estimates of abundance due to the longer length of time to decay until less than six pellets remain vs. that based on a 'decayed' group containing less than 16 pellets. The problem is ameliorated to some degree because individual pellets within a group are all subject to the same environmental processes that determine their rate of decay, and hence decay lengths are expected to be positively correlated. This will lead to a reduction in the variance of decay times within a group, and hence a faster reduction from 16 to six pellets than would occur if they decayed independently. A new study of dung decay is planned to resolve the above inconsistency. None the less, this exemplifies the need for the establishment of consistent criteria for the recognition of pellet groups in the field.

Square or rectangular quadrats are often used to estimate deer density from clearance plot or standing crop counts of dung. In order to devise regional management schemes for deer populations, knowledge of deer abundance at small spatial scales (e.g. forest blocks or estates) is needed. However, the amount of effort required to carry out enough clearance plot or standing crop counts in each block, to ensure that accurate and precise density estimates are obtained, may be prohibitive. In areas where deer densities are low, a large number of plots would have to be surveyed in order to obtain estimates with adequate precision. In such cases, line transect dung surveys would probably be more cost effective. Although fewer plots would be required in areas where deer densities are high, the requirement to detect all dung within each plot may make the method inefficient relative to line transect surveys, in which field workers need not be certain of detecting pellet groups unless they are on the line. However, in areas of very high densities the identification of pellet groups may become difficult, in which case clearance plots are likely to be preferred. The inability to discern between pellet groups will result in fewer groups being detected, which in turn will lead to an underestimate of density. This appears to have occurred in the high-density blocks in Peeblesshire, where estimates of deer abundance did not agree with local knowledge and current cull levels (Deer Commission for Scotland, unpublished data).

Direct comparisons between methods are required for a thorough evaluation of the relative merits of each method and the circumstances under which a given method may be more appropriate than the others. For example, at higher densities, line transect methods in which the distance from the centre of each detected pellet group from the line is measured may become less efficient than strip transects, in which all pellet groups within a narrower belt are counted. A comparative study could allocate the same resources to each approach, and determine their relative efficiency. If feasible, the biases of the different methods could be compared in an experiment where the total deer population size within the survey area is known.

Although the methodology presented in this paper was described in the context of deer populations, it can be applied to other animals for which dung count methods are used to estimate their abundance. Examples include wild guinea pigs (Cassini & Galante 1992) and elephants (Barnes *et al.* 1995) and a number of other large vertebrates (Hill *et al.* 1997). The methodology is equally applicable to surveys of nests or other signs for which production and decay rates can be estimated. For example, apes are most easily monitored by surveying their nests (Plumptre 2000).

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References

Abernethy, K. (1994) The establishment of a hybrid zone between red and sika deer (genus *Cervus*). *Molecular Ecology*, **3**, 551–562.

Bailey, R.E. & Putman, R.J. (1981) Estimation of fallow deer (*Dama dama*) populations from faecal accumulation. *Journal of Applied Ecology*, **18**, 697–702.

Barnes, R.F.W., Blom, A., Alers, M.P.T. & Barnes, K.L. (1995) An estimate of the numbers of forest elephants in Gabon. *Journal of Tropical Ecology*, **11**, 27–37.

Bear, G.D., White, G.C., Carpenter, L.H., Gill, R.B. & Essex, D.J. (1989) Evaluation of aerial mark–resighting estimates of elk populations. *Journal of Wildlife Management*, **53**, 908–915.

Buckland, S.T. (1992) Review of deer count methodology. Unpublished report to the Scottish Office, Agriculture and Fisheries Department, Edinburgh, UK.

Buckland, S.T., Anderson, D.A., Burnham, K.P. & Laake, J.L. (1993) *Distance Sampling: Estimating Abundance of Biological Populations*. Chapman & Hall, London, UK.

Cassini, M.H. & Galante, M.L. (1992) Foraging under predation risk in the wild guinea pig – the effect of vegetation height on habitat utilization. *Annales Zoologici Fennici*, **29**, 285–290.

Chadwick, A.H., Ratcliffe, P.R. & Abernethy, K. (1996) Sika deer in Scotland: density, population size, habitat use and fertility – some comparisons with red deer. *Scottish Forestry*, **50**, 8–16.

Dzieciolowski, R.M. (1976) Roe deer census by pellet-group counts. *Acta Theriologica*, **21**, 351–358.

Efron, B. & Tibshirani, R.J. (1993) *An Introduction to the Bootstrap*. Chapman & Hall, London, UK.

Hill, K., Padwe, J., Bejyvagi, C., Bepurangi, A., Jakugi, F., Tykuarangi, R. & Tykuarangi, T. (1997) Impact of hunting on large vertebrates in the Mbaracayu reserve, Paraguay. *Conservation Biology*, **11**, 1339–1353.

Laake, J.L., Buckland, S.T., Anderson, D.R. & Burnham, K.P. (1993) *DISTANCE User's Guide*. Colorado Cooperative Fish and Wildlife Research Unit, Colorado State University, Fort Collins, CO.

Mayle, B.A. & Staines, B.W. (1998) An overview of methods used for estimating the size of deer populations in Great Britain. *Population Ecology, Management and Welfare of Deer* (eds C.R. Goldspink, S. King & R.J. Putman), pp. 19–31. Manchester Metropolitan University and Universities' Federation for Animal Welfare, Manchester, UK.

Mayle, B.A., Doney, J., Lazarus, G., Peace, A.J. & Smith, D.E. (1996) Fallow deer (*Dama dama* L.) defecation rate and its use in determining population size. *Supplemento Alle Ricerche Di Biologia Della Selvaggina*, **25**, 63–78.

Mitchell, B.D., Rowe, J.J., Ratcliffe, P.R. & Hinge, M. (1985) Defecation frequency in roe deer (*Capreolus capreolus*) in relation to the accumulation rates of faecal deposits. *Journal of Zoology*, **207**, 1–7.

Mitchell, B.D., Staines, B.W. & Welch, D. (1977) *Ecology of Red Deer: A Research Review Relevant to their Management in Scotland*. Institute of Terrestrial Ecology, Cambridge, UK.

Neff, D.J. (1968) A pellet group count technique for big game trend, census and distribution: a review. *Journal of Wildlife Management*, **32**, 597–614.

Plumptre, A.J. (2000) Monitoring mammal populations with line transect techniques in African forests. *Journal of Applied Ecology*, **37**, 356–368.

Plumptre, A.J. & Harris, S. (1995) Estimating the biomass of large mammalian herbivores in a tropical montane forest – a method of faecal counting that avoids assuming a steady-state system. *Journal of Applied Ecology*, **32**, 111–120.

Putman, R.J. (1984) Facts from faeces. *Mammal Review*, **14**, 79–97.

Ratcliffe, P.R. (1987) Red deer population changes and the independent assessment of population size. *Symposia of the Zoological Society of London*, **58**, 153–165.

Rogers, G., Julander, O. & Robinette, W.L. (1958) Pellet-group counts for deer census and range-use index. *Journal of Wildlife Management*, **22**, 193–199.

Rose, H. (1994) Scottish deer distribution survey 1993. *Deer*, **9**, 153–155.

Seber, G.A.F. (1982) *The Estimation of Animal Abundance and Related Parameters*. Griffin, London, UK.

Trenkel, V.M., Buckland, S.T., McLean, C. & Elston, D.A. (1997) Evaluation of aerial line transect methodology for estimating red deer (*Cervus elaphus*) abundance in Scotland. *Journal of Environmental Management*, **50**, 39–50.

Van Etten, R.C. & Bennett, C.L. (1965) Some sources of error in using pellet-group counts for censusing deer. *Journal of Wildlife Management*, **29**, 723–729.

White, G.C., Bartmann, R.M., Carpenter, L.H. & Garrott, R.A. (1989) Evaluation of aerial line transects for estimating mule deer densities. *Journal of Wildlife Management*, **53**, 625–635.

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