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Is driven transect sampling suitable for estimating red-legged partridge *Alectoris rufa* densities?

Rui Borralho, Francisco Rego & Pedro Vaz Pinto

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An omnibus procedure for Alectoris partridges density estimation is still lacking. The suitability of driven line and strip transect sampling for estimating red-legged partridge Alectoris rufa densities on mixed farmland, in southern Portugal, in March, May and July 1993 and 1994 was evaluated. Driven transect counts along a grid of dirt tracks were performed and compared to early spring territory mapping counts. Distance data sets exhibited prominent peaks near the origin, apparently caused by attraction of the birds to the tracks; nevertheless, line transect estimates computed using Fourier series models were similar to mapping counts in March of both years, as well as adult density estimates in July, but density was underestimated in May 1994. Line transect estimates were robust to the shift from individuals to clusters as sighting units, and to different grouping options, but not to data truncation. Driven strip transect estimates were computed using 10 m, 20 m, 40 m, 80 m, and 160 m strip widths. In March, estimates computed using the first three widths overestimated density and underestimated it in 1994 when the 160-m strip was used. May and July adult density estimates were not significantly different from those in March. In this study, driven line transect sampling was an efficient and accurate method of estimating red-legged partridge density on a farmland area in early spring and summer; however, further research is needed to evaluate its suitability in habitats of lower visibility, as detection models seem to require long-distance sightings to compensate for the attractiveness of tracks. Strip transects are not recommended because of the difficulty of choosing an adequate strip width for density estimation. Both methods revealed similar utility as indices of relative population abundance.

Key words: Alectoris rufa, driven transect, line transect, mixed farmland, Portugal, red-legged partridge, strip transect

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Alectoris partridges are gamebirds of high economic importance in large areas of the Palearctic and Nearctic, inducing a considerable research effort on their biology and management (e.g. Birkan et al. 1992 and references therein). Adequate population estimation methods are critical for both research and management purposes. However, even though a large range of methods has been used for density estimation (Pépin 1983, Lucio & Purroy 1985, Tapper 1988, Ricci 1989, Nadal et al. 1990, Birkan 1991), there is still no tested accurate and efficient procedure, robust enough for application throughout the year and in all habitats where *Alectoris* species are found. Line transect theory and inherent density estimation procedures (Burnham et al. 1980, Buckland et al. 1993) could possibly fulfill this role. Nevertheless, although counting techniques relying on transect sampling have been used, such as strip

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transects (Lucio & Purroy 1985) and encounter rate correlations with territory mapping estimates (Ricci 1989), the theoretically more reliable line transect estimation (Burnham & Anderson 1984, Burnham et al. 1985) has never been employed because of perceived behavioural incompatibilities with the assumptions of the method (Anderson et al. 1979, Burnham et al. 1980).

Strip transects are in fact elongated plots with fixed areas, to which classical finite population sampling theory applies. Line transects extend this approach by modelling the detectability of the target-organisms through the inclusion of detection distances in the analyses. Unlike finite sampling theory, when using distance sampling the size of the sample area is sometimes unknown, and many objects can remain undetected. Theoretically, unbiased estimates of density can be made from these distance data if certain assumptions are met. Line transect theory relies on three main assumptions, given in order of importance from most to least critical (Buckland et al. 1993): 1) objects directly on the line are detected with certainty; 2) objects are detected at their initial location and do not move before being detected; and 3) distances and angles are measured accurately. It is also critical that the lines are placed randomly with respect to the distribution of objects (Buckland et al. 1993), although this should not be regarded as an assumption but rather as a field sampling guideline. Anderson et al. (1979) and Burnham et al. (1980) pointed out that chukar partridges Alectoris chukar tend to run rather than flush and to assemble in loose groups, as do other Alectoris species, implying probable violation of all or some of the main assumptions; thus they recommended that line transects should not be used for density estimation of these birds without additional information.

We studied the suitability of driven line and strip transect sampling for estimating red-legged partridge Alectoris rufa densities in mixed farmland, during the breeding seasons of 1993 and 1994. A priori the use of a car as the observation platform should convey a number of advantages: 1) the car serves as a hide (Green 1983), as partridges react less to vehicles than to persons, reducing evasive behaviour; 2) observers in a car move faster than by walking, reducing the relative importance of partridge movement (Turnock & Quinn 1991); and 3) using a car increases the total distance travelled, improves visibility and reduces observer fatigue, allowing the collection of a larger sample in less time, potentially increasing the precision of the estimates (Anderson et al. 1979). The first two advantages will tend to compensate for the reactive movement of the partridges, but none solves the measurement problems induced by the loose structure of partridge clusters. However, these will vary with time of year (Green 1983) and can potentially be minimised by judicious grouping of the distance data. On the other hand,

the use of a vehicle entails some limitations: 1) in most areas it forces the researchers to place the transect lines in a non-random manner, frequently along tracks (Redmond et al. 1981, Andersen et al. 1985); and 2) some of the transect lines will not be straight, potentially reducing accuracy and precision (Smith & Nydegger 1985).

Concurrently with driven transect sampling, we performed intensive territory mapping counts, arguably the most accurate of the available methods of red-legged partridge density estimation (Pépin 1983). Our objectives were to: 1) compare driven line and strip transect density estimates with territory mapping counts; 2) evaluate the effect of season (early spring, mid spring, and early summer); 3) evaluate the effect of unit of analysis, data grouping and data truncation on line transect analyses; and 4) examine the extent to which our driven transect estimates of partridge density meet the critical assumptions of line transect density estimation.

Study area

The study site was a 19.84 km² agricultural farm situated at 38°30'N and 7°39'W in Alto Alentejo, southern Portugal. The terrain is mostly flat, ranging in altitude from 210 to 255 m a.s.l. The climate is Mediterranean-like with hot dry summers and mild winters; average annual temperature is 15.6°C and average annual total rainfall is 642.6 mm (Instituto Nacional de Meteorologia e Geofísica 1991). Vegetation was dominated by cereal crops (about 25% of the area), grasslands (20%) grazed by cattle and sheep, cork oak Quercus suber and holm oak Quercus rotundifolia stands (18%), abandoned rice fields (14%), and olive tree Olea europea groves (5%). A reservoir covered 0.3 km² in the spring of 1993 and 0.76 km² in the spring of 1994, and a residential area occupied 0.09 km² in both years, so we computed an 'effective area' for partridge abundance estimation of 19.45 km² in 1993 and 18.98 km² in 1994. The area was quite uniformly traversed by dirt tracks.

The farm was a private game estate, the red-legged partridge population being managed for game exploitation. In the hunting season of 1992/93 (fall/winter) the partridges were not hunted, but in the hunting season of 1993/94 they were. This could have caused differences in the amount of reactive movement occurring during the transect counts.

Methods

Data collection

Towards the end of the breeding season territories begin

to break down and accuracy of mapping counts declines (e.g. Franzreb 1976); we, therefore, conducted territory mapping counts at the beginning of the breeding season, in March/April 1993 and 1994. In March, May and July of both years we also performed driven line and strip transect surveys for a total of six 10-day periods. These periods corresponded to the time of peak pair formation, incubation, and post-brood-rearing, respectively (our own unpubl. data).

Territory mapping

After a preliminary reconnaissance and mapping of prominent topographic features and objects, we divided the study area into 1-km² plots, which were intensively and similarly surveyed during the first three hours after dawn and preceding dusk, both by observers using a fourwheel-drive vehicle and by walking observers. Observers plotted the locations of partridge sightings, calling birds, tracks, and droppings on 1:15,000 aerial photographs and 1:25,000 topographic maps, recording the number and behaviour of detected individuals and the habitat associated with each location. Daily location maps were generated through this procedure. We also performed focal sampling of specific individuals and pairs to gather additional information on territorial boundaries and interactions with neighbouring birds. Mapping counts were stopped when the cumulative number of detected pairs plotted against cumulative searching effort reached an asymptote, i.e., once no new territory was detected within reasonable time limits (Fig. 1).

Driven transects

Transects were dirt tracks or jeep trails allowing identification of the center line at all times, although a few were not entirely straight. For practical reasons, random sampling of the study area was not possible; instead transect lines were placed so that previously mapped land-use



Figure 1. Field search effort of early spring territory mapping counts of red-legged partridges on mixed farmland in southern Portugal, 1993-94. In 1993, 80 pairs and three isolated individuals were detected, and in 1994, 146 pairs and 12 isolated partridges were detected.

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classes were sampled in proportion to availability (Buckland et al. 1993). Total transect length sampled in each survey ranged from 19.74 km to 64.05 km.

Two observers drove along the transects in a fourwheel-drive vehicle at a speed of 10-20 km/hr, during the first three hours after dawn and in good weather conditions (avoiding periods of rain and high wind). To minimise the risk of missing any birds positioned directly on the center line, both the driver and the passenger surveyed it; the driver also surveyed the left side of the transects and the passenger the right side. The observers recorded 1) estimated perpendicular distances to the perceived geometric center of sighted clusters (≥ 1 individuals); 2) cluster size; 3) habitat where the clusters were first seen; 4) transect number; and 5) starting and ending times of surveys. Distances were visually estimated. Prior testing revealed that observers estimated distances accurately to the nearest 1-m up to 5 m from the center line, to the nearest 2-m up to 10 m away, to the nearest 5-m up to 50 m away, to the nearest 10-m up to 70 m away, to the nearest 15-m up to 100 m away, and to the nearest 30-m up to 160 m; we adopted these levels of precision as default grouping classes.

Before running the transects, observers trained visual distance estimation and recorded tape-measured distances to prominent features along the survey tracks for use as references in the field. We selected visual distance estimation to avoid triggering a response movement of previously undetected birds while measuring distances with a tape. Probably, range finder measurements would also avoid this response, however, in a pilot survey we verified that our visual estimates were three times faster than range finder measurements and were not significantly different from them (paired t-test, $t_{30} = 1.34$, P > 0.05).

Data analyses

Territory mapping

From the daily location maps we compiled composite maps of the partridge locations for the beginning of each breeding season. We interpreted these composite maps and delineated individual territories using a range of 5-26 independent recordings, and our knowledge of the topography, vegetation, and human disturbance in the area.

Line transects

Line transect estimates and confidence intervals were computed using the DISTANCE (Laake et al. 1993) computer program. In the exploratory phase of the analysis we used a variety of recommended robust models as implemented by DISTANCE (Buckland et al. 1993), and we verified that for our data sets the Fourier series model (i.e. uniform key function with cosine series expansion, Buckland et al. 1993) consistently performed best, being more robust and providing less biased estimates, compared with mapping counts, than the other tested estimators. Accordingly, the results and discussion presented here are limited to the Fourier series detection model.

In the default analysis we used 1) individuals as sighting units; 2) the default grouping classes indicated above, after eliminating empty classes by pooling; and 3) untruncated perpendicular distance data. Default procedures considered individual animals because only three of the six data sets were large enough to allow an *a priori* reliable analysis based on clusters (Buckland et al. 1993, Sherman et al. 1995); this possibly caused underestimation of variances. Using mapping counts as reference, we examined the relative bias of March counts by computing percent relative bias as PRB = $100(\hat{D} - D)/D$, where \hat{D} was the density estimated through transect sampling, and D was the mapping count density. We compared mapping and March transect estimates by Student's ttests. To check for spurious estimates of D in July, we derived adult density $\hat{D}_{ad} = \hat{D} \times R_{ad}$, where R_{ad} was the adult/total ratio of sighted partridges, both along and outside the transects, during the July survey periods; in 1993 $R_{ad} = 0.315 \ (\pm SE = 0.013)$ and in 1994 $R_{ad} = 0.296$ (± 0.003) (our own unpubl. data). Variance (var) of \hat{D}_{ad} was calculated as $\hat{D}^2 \operatorname{var}(R_{ad}) + R_{ad}^2 \operatorname{var}(\hat{D}) - \operatorname{var}(\hat{D})$ var(R_{ad}), where the product of variances is subtracted because estimates of variances are being used (Goodman 1960). We tested for differences between March and May estimates and between March estimates and July adult density estimates, using t-tests.

Even though we computed density estimates using clusters as analytical units for all data sets (see Table 2), all the comparisons with cluster-based estimates were performed considering exclusively the data sets of March 1993, May 1993, and March 1994 (i.e. ≥19 clusters data sets), as the minimum sample size allowing reliable line transect estimates reported in the literature is 20 (Sherman et al. 1995), and the low precision of the remaining estimates would greatly reduce the power of the tests. We examined the existence of cluster size bias with DISTANCE's size-bias regression (option gxlog), using the mean cluster size if this was not significant (P > 0.05)and the corrected expected cluster size if it was. We computed PRBs for March estimates derived using the default grouping and untruncated data and we compared line transect estimates based on clusters as analytical units to mapping counts through t-tests; the degrees of freedom of cluster-based line transect estimates of partridge density (individuals/area) were computed by DISTANCE taking into account not only the number of clusters sighted but also the number of individuals of those clusters (Buckland et al. 1993), resulting in a number of degrees of freedom higher than the number of clusters detected. Considering the whole range of grouping options tested (see below), we used paired t-tests to compare point estimates and coefficients of variation (CV) calculated using individuals and clusters as analytical units (18 pairs of estimates).

In addition to the default data grouping, we tested five more grouping procedures: 1) ungrouped data, 2) data grouped by 5-m intervals, 3) 10-m intervals, 4) 20-m intervals, and 5) 30-m intervals. We calculated PRBs for the March estimates derived through all the grouping options, using individuals as units and untruncated data; relative accuracy was evaluated comparing line transect estimates with mapping counts through t-tests. For all data sets, we compared point estimates and CVs computed using default grouping with the ones calculated using the other grouping options, through paired t-tests.

We arbitrarily considered two ranges of data truncation, i.e. 2-7%, and 8-15%. Using individuals as analytical units and default grouping, we computed PRBs of March density estimates at both truncation levels and evaluated their relative accuracy comparing data-truncated estimates with mapping counts through t-tests. Considering all data sets, we compared point estimates and CVs of each truncation option between each other and with default density estimates using paired t-tests.

Since models with high number of terms can give rise to unrealistic shapes for the detection function (Buckland 1985), we used DISTANCE's 'maxterms' option to force the program to generate models with less than four terms. We checked the goodness of fit of all detection models using DISTANCE's χ^2 goodness of fit statistic.

Strip transects

For strip transect density estimation we considered transects as unequal-size sample units, and five strip widths (10 m, 20 m, 40 m, 80 m and 160 m) with a half-width on each side of the transect lines. We computed point estimates and confidence intervals following standard ratio method procedures for sampling without replacement (e.g. Krebs 1989). We calculated PRB for each March strip estimate and evaluated relative bias through t-tests, and compared March estimates to May and July adult density estimates (computed from overall density as indicated above) by paired t-tests. We checked for differences between density estimates and CVs computed using different strip widths through paired t-tests. To evaluate if there was any consistent trend in the precision of the estimates as strip width increased, we used linear regression to correlate CVs with strip widths for each data set.

We compared strip and default line transect point estimates through paired t-tests, and used linear regression to assess if strip and line transect estimates exhibited similar trends across the study period and, hence, revealed similar utility as indices of relative population abundance.

Table 1. Time spent (man-hours) performing early spring territory mapping and default driven transect estimates of red-legged partridge density on mixed farmland in southern Portugal, 1993-94.

| Year | Method | Pre-survey preparation | Data collection | Data analyses | Total |
|------|-------------------|---------------------------|-----------------|------------------|-------|
| 1993 | Territory mapping | g 10 | 87 | 4 | 101 |
| | Driven transects | 12 | 14 | 2 | 28 |
| 1994 | Territory mapping | g 4 | 159 | 6 | 169 |
| | Driven transects | 2 | 22 | 2 | 26 |

We did not test for differences between CVs, as default line transect estimates overestimated precision.

Results

Count effort

Considering the pre-survey preparatory tasks, data collection, and data analyses, the overall territory mapping surveys took $3.6\times$ more time to perform than driven transects (default options) in March/April 1993, and $6.5\times$ more time during the equivalent period in 1994 (Table 1). The difference between the periods resulted mostly from the longer time necessary in 1994 to attain the asymptotic stage of territory detection (see Fig. 1) due to higher partridge density, and from the less time necessary in 1994 to execute the pre-survey tasks of transect counts. With minor circumstantial differences, the same time was spent computing default line as strip transect estimates.

Territory mapping

At the beginning of the breeding season of 1993, 163 partridges were censused (80 pairs and 3 isolated individuals), corresponding to a density of 8.38 partridges/km²; in 1994, 304 individuals were counted (146 pairs and 12 isolated partridges), corresponding to a density of 16.01 birds/km².

Line transects

Sighting data

All samples comprised at least 30 sightings of individual partridges, three of them comprising more than 40. Three of the data sets comprised \leq 15 cluster sightings, the remaining three comprised 19, 23, and 41 cluster sightings. We were able to compute non-spurious density estimates (i.e. not disproportionately high or low estimates) from the \geq 19 sightings samples (Table 2), which agrees with the results presented by Sherman et al. (1995).

All detection histograms exhibited a noticeable peak at the first distance interval (Fig. 2), with no prominent peaks in the second or third intervals attributable to partridges' reactive movement. Of a total of 66 Fourier series models considered here only seven did not have a significantly poor fit (P > 0.05), and five of these were derived from the sample of July 1994, the less 'spiked' of the data sets; in the exploratory phase of the analysis we verified that all recommended robust estimators available in DISTANCE generated models with overall similar poor fits (our own unpubl. data).

Default analysis

Default density estimates (see Table 2) of March line transect surveys were very similar to territory mapping counts ($t_{34} = 0.11$ for 1993, $t_{73} = 0.29$ for 1994, P > 0.05 for both years), with 1993's point estimate being slightly lower and 1994's slightly higher than mapping results. May's point estimate was 26.3% lower than March's estimate in 1993, and 52.2% lower in 1994, although only the latter

Table 2. Default driven line transect estimates of red-legged partridge density on mixed farmland in southern Portugal, 1993-94. Density values were computed through Fourier series analyses of grouped, untruncated perpendicular distance data.

| Survey | Unit | Number of sightings | Birds/km ² | SE | %CV | 95% CI | % relative bias1 |
|------------|------------|---------------------|-----------------------|-------|------|---------------|------------------|
| March 1993 | Individual | 36 | 8.22 | 1.49 | 18.1 | 5.71 - 11.84 | -1.9 |
| | Cluster | 19 | 8.22 | 2.07 | 25.2 | 4.92 - 13.75 | -1.9 |
| May 1993 | Individual | 35 | 6.06 | 1.07 | 17.7 | 4.24 - 8.67 | |
| | Cluster | 23 | 5.97 | 1.39 | 23.3 | 3.76 - 9.48 | |
| July 1993 | Individual | 42 | 25.03 | 4.13 | 16.5 | 17.97 - 34.87 | |
| | Cluster | 7 | 12.52 | 5.81 | 46.4 | 4.25 - 36.90 | |
| March 1994 | Individual | 76 | 16.61 | 2.09 | 12.6 | 12.95 - 21.31 | 3.7 |
| | Cluster | 41 | 16.76 | 2.92 | 17.4 | 11.85 - 23.71 | 4.6 |
| May 1994 | Individual | 30 | 7.94 | 1.60 | 20.2 | 5.28 - 11.96 | |
| | Cluster | 15 | 5.20 | 1.78 | 34.1 | 2.64 - 10.27 | |
| July 1994 | Individual | 113 | 50.85 | 5.90 | 11.6 | 40.50 - 63.84 | |
| | Cluster | 12 | 35.21 | 12.65 | 35.9 | 16.98 - 72.99 | |

¹ Percent relative biases were calculated using territory mapping counts as reference, and were computed for March estimates only as towards the end of the breeding season territories begin to break down and accuracy of mapping counts declines (e.g. Franzreb 1976).

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Figure 2. Detection histograms for driven transect surveys of red-legged partridges on mixed farmland in southern Portugal, 1993-94. Sightings are grouped in 10-m intervals.

difference was statistically significant ($t_{67} = 1.18$, P > 0.05 for 1993, $t_{100} = 3.29$, P = 0.001 for 1994). In July 1993 the estimated adult density was 7.89 adults/km² (± SE = 1.32), and in July 1994 it was 15.07 adults/km² (± 1.78); these estimates were not significantly different from the March estimates ($t_{75} = 0.17$ for 1993, $t_{185} = 0.56$ for 1994, P > 0.05 for both years), adult point estimates in July being 4.1% (1993) and 9.3% (1994) lower than March estimates (Fig. 3).



Figure 3. Territory mapping and default driven line transect density estimates of red-legged partridges on mixed farmland in southern Portugal, 1993-94. Horizontal lines represent early spring mapping counts, and bars (+SE) represent default line transect estimates.

Unit of analysis

No cluster size bias was detected in any data set (P>0.05). March estimates computed using clusters as analytical units were not different from mapping estimates ($t_{22} = 0.08$ for 1993, $t_{57} = 0.25$ for 1994, P>0.05 for both years), and had PRBs similar to the ones assessed using individual partridges as units (see Table 2). Density point estimates derived from samples of clusters and of individuals were not significantly different (paired t-test, $t_{17} = 0.69$, P>0.05). Conversely, estimated precision of cluster analysis was significantly lower than that of individual analysis (paired t-test, $t_{17} > 1000$, P < 0.001), with $\overline{CV}= 22.2\%$ (± 0.8) for the former, and $\overline{CV}= 16.2\%$ (± 0.6) for the latter.

Data grouping

Considering all the grouping options tested in both years, there were no significant differences between any March line transect estimates (Table 3) and mapping estimates ($t_{34} \le 0.33$ in 1993, $t_{73} \le 0.33$ in 1994, P > 0.05 in both years). Average PRB was 3.1% (± 1.5) in 1993 and 3.7% (± 0.2) in 1994; as a whole, 1993's and 1994's March estimates were similarly biased ($t_{10} = 0.39$, P > 0.05). No set of point density estimates generated through any grouping procedure was significantly different from the

| Survey | Grouping intervals | Number of sightings | Birds/km ² | SE | %CV | 95% CI | % relative bias |
|------------|--------------------|---------------------|-----------------------|------|------|---------------|-----------------|
| March 1993 | Ungrouped | 36 | 8.23 | 1.45 | 17.6 | 5.78 - 11.72 | -1.8 |
| | 5-m | 36 | 8.91 | 1.60 | 18.0 | 6.20 - 12.81 | 6.3 |
| | 10-m | 36 | 8.91 | 1.60 | 18.0 | 6.20 - 12.81 | 6.3 |
| | 20-m | 36 | 8.91 | 1.60 | 18.0 | 6.20 - 12.81 | 6.3 |
| | 30-m | 36 | 8.65 | 1.57 | 18.1 | 6.01 - 12.45 | 3.2 |
| March 1994 | | | | | | | |
| | Ungrouped | 76 | 16.74 | 2.17 | 13.0 | 12.94 - 21.65 | 4.5 |
| | 5-m | 76 | 16.61 | 2.09 | 12.6 | 12.94 - 21.33 | 3.2 |
| | 10-m | 76 | 16.51 | 2.08 | 12.6 | 12.85 - 21.19 | 3.1 |
| | 20-m | 76 | 16.57 | 2.09 | 12.6 | 12.91 - 21.28 | 3.5 |
| | 30-m | 76 | 16.66 | 2.10 | 12.6 | 12.98 - 21.39 | 4.0 |

Table 3. Early spring driven line transect estimates of red-legged partridge density on mixed farmland in southern Portugal, 1993-94, computed using different data grouping procedures.

set of default estimates (paired t-tests, $t_5 \le 2.27$, P > 0.05), and the same applies to CVs (paired t-tests, $t_5 \le 1.65$, P > 0.05).

Data truncation

Percent relative biases of density estimates computed from truncated data were high in both years (Table 4), although these estimates were significantly different from mapping counts only in 1994 (in 1993 $t_{32} = 1.33$ for level 1, and $t_{30} = 1.99$ for level 2, P > 0.05 for both levels; in 1994 P < 0.001 for both truncation levels). Tests comparing default point estimates with data truncated estimates were significant for both truncation levels (paired t-tests, $t_5 = 2.72$ for level 1, $t_5 = 2.71$ for level 2, P < 0.05 for both), but the test was non-significant when the truncation levels were compared to each other (paired t-test, $t_5 = 2.21, P > 0.05$). Precision of default estimates was consistently higher than that of data truncated estimates (paired t-tests, $t_5 = 2.68$ for level 1, $t_5 = 3.23$ for level 2, P < 0.05 for both levels), and precision of level 1 estimates was higher than that of level 2 estimates (paired ttest, $t_5 = 3.18$, P < 0.05).

Strip transects

In both years, March strip transect counts overestimated

density when the 10-m, 20-m, and 40-m strip widths were used ($t_{39} \ge 2.15$, P < 0.05); conversely, in 1994 the density was underestimated when the 160-m strip width was adopted ($t_{60} = 7.79$, P < 0.001). No significant biases were detected neither for the 80-m strip transect estimates $(t_{39} = 0.84, P > 0.05 \text{ for } 1993, t_{60} = 0.87, P > 0.05 \text{ for } 1994),$ nor for the 160-m strip transect estimate ($t_{30} = 1.50$, P > 0.05) of 1993, although their PRBs ranged from -24.7% to 24.0% (Table 5). May estimates and July adult density estimates were not significantly different from March estimates (paired t-tests, $t_4 \le 2.66$, P > 0.05), in both years. Conversely, all sets of density point estimates computed using a particular strip width were significantly different from any other set of estimates derived using dissimilar strip widths (paired t-tests, $t_5 \ge 3.95$, P < 0.05); and, with the exception of the pair 10-m/20-m of strip transect estimates (paired t-test, $t_5 = 2.33$, P > 0.05), the precision of the estimates was significantly different when considering different strip widths (paired t-tests, $t_5 \ge 2.67$, P < 0.05), increasing as strip width increased in all data sets $(r_4 \ge 0.899, P < 0.05).$

Default line transect density estimates were significantly lower than 10-m (paired t-test, $t_5 = 6.94$, P < 0.001) and 20-m (paired t-tests, $t_5 = 4.88$, P = 0.005) strip transect estimates; no significant differences were detected relative to the other sets of strip transect estimates (paired t-tests,

Table 4. Early spring driven line transect estimates of red-legged partridge density on mixed farmland in southern Portugal, 1993-94, computed from distance-truncated data.

| Survey | W*1 (m) | Data truncation (%) | No of sightings | Birds/km ² | SE | %CV | 95% CI | % relative bias |
|------------|------------|------------------------|-----------------|-----------------------|------|------|---------------|-----------------|
| March 1993 | 80 | 5.55 | 34 | 11.20 | 2.12 | 18.9 | 7.65 - 16.39 | 33.6 |
| | 65 | 11.11 | 32 | 13.49 | 2.55 | 18.9 | 9.20 - 19.78 | 60.9 |
| March 1994 | 60 | 3.95 | 73 | 30.25 | 4.11 | 13.6 | 23.10 - 39.62 | 88.9 |
| | 45 | 14.47 | 65 | 37.47 | 5.21 | 13.9 | 28.43 - 49.39 | 134.0 |

¹ Truncation distance.

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Table 5. Early spring driven strip transect estimates of red-legged partridge density on mixed farmland in southern Portugal, 1993-94.

| Survey | Strip width (m) | Number of sightings | Birds/km ² | SE | %CV | 95% CI | % relative bias |
|------------|--------------------|---------------------|-----------------------|-------|------|----------------|--------------------|
| March 1993 | 10 | 23 | 68.30 | 21.04 | 30.8 | 25.77 - 110.83 | 714.9 |
| | 20 | 23 | 34.15 | 10.45 | 30.6 | 13.06 - 55.24 | 307.5 |
| | 40 | 26 | 19.30 | 5.08 | 26.3 | 9.04 - 29.56 | 130.3 |
| | 80 | 28 | 10.39 | 2.39 | 23.0 | 5.56 - 15.23 | 24.0 |
| | 160 | 34 | 6.31 | 1.38 | 21.8 | 3.53 - 9.09 | -24.7 |
| March 1994 | 10 | 42 | 79.96 | 16.31 | 20.4 | 47.18 - 112.06 | 397.2 |
| | 20 | 51 | 48.34 | 9.23 | 19.1 | 29.85 - 66.83 | 201.9 |
| | 40 | 55 | 26.07 | 4.48 | 17.2 | 17.08 - 35.05 | 62.8 |
| | 80 | 60 | 14.22 | 2.06 | 14.5 | 10.09 - 18.35 | -11.2 |
| | 160 | 73 | 8.65 | 0.94 | 10.9 | 6.76 - 10.54 | -46.0 |

 $t_5 \le 2.11$, P > 0.05). Strip and line transect point estimates displayed significantly similar trends across the study period, irrespective of strip width ($r_4 \ge 0.812$, P < 0.05).

Discussion

Attractiveness of transects

Since systematic underestimation of sighting distances by the observers was not detected in pilot surveys (see Methods), the prominent peaks of all detection histograms at first distance intervals (see Fig. 2) and the noticeably high narrow-strip transect density estimates, seem to indicate that the dirt tracks used as transects attracted the partridges, producing a gradient of partridge density perpendicular to transect lines or, alternatively, that the birds moved towards the observers during the transect counts. The latter possibility is improbable since the usual reaction of gamebirds to humans is to move away or to freeze, and we never detected any deliberate movement towards the 'sampling vehicle'; thus, the former prospect is much more likely. Attractiveness of tracks could derive from factors such as proximity to preferred breeding cover, availability of grit for ingestion and dust-bathing purposes, or avoidance of wet vegetation in early morning.

Aggregation of birds along the transects might imply overestimation of density, and to orient transect lines parallel to density profiles may increase the variance of \hat{D} (White et al. 1989). Both attraction to and avoidance of tracks by sampled populations have been reported (e.g. Buckland 1985, Varman & Sukumar 1995), and this should be acknowledged as a potential limitation of driven transect sampling in areas where the vehicles cannot freely cross most of the study sites, as in farmland, and where the tracks and their surroundings may constitute a separate habitat for the target species, which should be the case for the red-legged partridge in our study area. In areas where the sampled trails do not represent a habitat discontinuity for the studied population this problem should not arise (Andersen et al. 1985).

Line transects

In both years, default line transect estimates were similar to territory mapping results in early spring and were consistent with these counts in early summer. Available evidence, however, appears to indicate that transect sampling tends to underestimate partridge density during the incubation and brood-rearing periods, a feature previously detected for other land-nesting birds (Redmond et al. 1981). Hence, although we should be aware that territory mapping counts are also subject to error and bias (e.g. Best 1975), these results indicate that driven line transect counts of breeding red-legged partridges in farmland are as accurate as mapping counts and much more efficient, even though line transect sampling is probably not appropriate during the incubation and brood-rearing periods. On the other hand, several of our estimates have relatively low precision, even though we probably underestimated variances by using individuals as sample units (Buckland et al. 1993), and by fitting Fourier series models to the sighting data (Buckland 1982). Higher precision would be attainable with larger samples (Kelley 1996), but in areas with low partridge densities this may considerably increase the sampling costs and reduce the relative advantage of line transect sampling over territory mapping.

It seems that the high relative accuracy of the estimates coexisted with the attractiveness of the tracks at the expense of generally poor fits of the models. Fourier series models normally have difficulty fitting peaked data sets (Buckland 1985). However, for several of our samples a good fit would probably have implied overestimation of partridge density. Even though our models consistently provided accurate estimates in early spring and summer, and a significantly poor fit need not be of great concern (Buckland et al. 1993), when there are no independent estimates to evaluate the accuracy of line transect estimates a poor fit will normally lead to the rejection of the model. Thus, the general applicability of the tested driven line transect procedures remains in doubt until enough empirical evidence is gathered that they consistently provide accurate estimates.

Available evidence from this study concerns only open farmland-like habitats. The method may not be applicable in areas with lower visibility, where almost all birds are detected near the transect lines. In fact, the low accuracy of data-truncated estimates may indicate that the tested models need 'external' sightings to compensate for the peak of observations near the transects. Unlike data truncation, the shift of analytical units from individuals to clusters, and the use of different data grouping options, did not affect the accuracy of density estimation, although estimated precision was lower when clusters were used. Likewise, even though partridge density doubled from 1993 to 1994 due to the implementation of shooting restrictions and game management actions (our own unpubl. data), this did not seem to affect the accuracy of the estimates. This robustness broadens the procedures of data collection and analysis, and increases the number of situations where this method is applicable.

Although the attractiveness of transects to the counted animals does not respect line transect theory, the three main assumptions of the method did not seem to be seriously violated during most of the sampling periods. All, or almost all, birds positioned directly on transect lines should have been detected, as most center lines had excellent visibility. Nevertheless, the underestimation of density in May could be attributable to birds situated near the transect being missed, possibly because the partridges were on nests inside the vegetation bordering the tracks or were better concealed. There was no evidence for significant partridge reactive movement in either year, irrespective of the fact that the population was hunted in the 1993/94 hunting season. Finally, distances were visually estimated, not measured accurately, but data grouping should have compensated at least partly for this.

Driven line transect sampling apparently solved any potential problems related to the reactive movement of partridges, and did not seem affected by the loose structure of partridge clusters, allowing accurate partridge density estimation in a fairly open agricultural landscape. Yet the impossibility of vehicles randomly crossing many of the potential study areas induces a different problem that should be investigated before attempting to generalise the method to other habitats, particularly habitats of low visibility. Research on this can concentrate on: 1) evaluating driven line transect sampling in separate environments; 2) on post-sampling correction of the density gradient induced by track attractiveness, by exploring (for example) approaches similar to the ones suggested by Turnock & Quinn (1991) to compensate for responsive movement toward the observers; or 3) on testing other ways of traversing the transects that potentially do not trigger the reactive movement of the partridges and simultaneously allow random sampling of the area, such as horseback line transect sampling.

Strip transects

The expected pattern of unbiased narrow strip transect density estimates (Burnham et al. 1985) did not occur; instead narrow strip estimates overestimated partridge density probably as a consequence of track attractiveness. Wide strip transect estimates tended to underestimate density as expected, and only the 80-m strip estimates did not significantly differ from mapping counts in both years. Usually two kinds of errors are possible during strip transect sampling (Pépin & Birkan 1981): 1) the number of animals detected inside the strip may be different from the real number of animals present at that moment, and 2) the strip width used for calculations may be different from the real sampled width. The first source of bias will tend to underestimate density owing to visibility problems, but the second can contribute to overestimation if the observers decide more frequently that an animal is flushed inside the strip than outside. In our case, however, the second type of error should not have been systematic since an estimated distance was assigned to each sighting, irrespective of any strip width, and no systematic underestimation of distances was detected in pilot surveys.

For a similar sampling effort, and using the mapping counts as reference, all strip transect point estimates were less accurate than line transect estimates. A relative gain in efficiency is possible if instead of estimating the perpendicular distance to every sighting the observers have to decide only if a given animal or cluster is situated inside or outside a strip. Nevertheless, even though one of the strip widths allowed fairly accurate estimation of partridge density, the choice of the adequate width is a difficult task (Burnham & Anderson 1984, Burnham et al. 1985), and is worsened by the detected density gradient perpendicular to transect lines, reducing the usefulness of strip transect sampling when no other method is simultaneously used for independent density estimation. However, if one is only interested in monitoring partridge populations by using indices of relative population abundance, this latter possibility would give some minor advantages to strip transects over line transect counts, since this option would slightly reduce the strip transect sampling time, and their estimates revealed similar value as indices of relative abundance irrespective of strip width. Acknowledgements - we are grateful to N.J. Aebischer, S.T. Buckland, J.F. Bugalho, F. Palomares, D. Stauffer, C. Stoate, and two anonymous referees for reviewing earlier versions of the manuscript, and to A. Torres for allowing us to conduct this study on his property. We gratefully acknowledge the financial support provided by JNICT through the project STRD/AGR/0137 and through the grants BD/1628/91 and BD/3847/94, and provided by INIA and IF-ADAP through the project PAMAF-4030.

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