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Spotlight counts for assessing abundance of rabbits (*Oryctolagus cuniculus* L.)

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Abstract

We determined the precision of spotlight counts of rabbits *(Oryctolagus cuniculus* L.) and their accuracy as estimates of density, by making counts from a motorcycle along 17 1-km transects in the Mackenzie Basin, New Zealand. Rabbits were poisoned and density per 1-ha quadrat was measured. Precision of spotlight counts would be between 5–28% and 6–39%, using impracticably large numbers of counts, even allowing for the effects of snow and heavy rain, observer bias and number of runs per night. Spatial and unexplained variance would result in even less precise counts using 25 transects and 1–5 nights. Actual rabbit densities explained only 41% of the variance in spotlight counts. Confidence intervals of absolute rabbit densities are extremely large, especially when observed counts are high. At best, spotlight counts could be used to detect differences in actual rabbit abundance spanning an order of magnitude or more. Observed reduction in spotlight counts is likely to underestimate reduction in actual density because the spotlight count index ‘saturates’ at high rabbit density. However, spotlight counts along fixed transects before and after a control operation can be used to estimate percentage kill with acceptable precision if the kill rate is at least 80%.

Introduction

The European rabbit, *Oryctolagus cuniculus* (L.), is a serious pest in parts of New Zealand and Australia. It has caused changes in the composition of native grasslands, has aggravated erosion (Gibb and Williams 1994), and threatens agricultural production (Croft 1990; Norbury and Norbury 1996). The effective control of this species requires reliable indices of abundance. These allow managers to target areas in need of rabbit control, to measure the efficiency and cost-effectiveness of control measures, and to plan the overall expenditure on rabbit control. The need for a reliable measure of change in rabbit density is now paramount in view of the recent release of Rabbit Calicivirus Disease (RCD) in Australia and New Zealand. Measures of the initial reduction and subsequent resurgence in rabbit abundance following RCD release are crucial for assessing the efficacy of the ensuing biological control and the potential effects on predators and other wildlife (Barlow and Kean 1996).

Amongst the various methods used to assess rabbit populations, night-time counting using spotlights along fixed transects has become the standard method used by the Ministry of Agriculture and Fisheries and by Regional Councils in New Zealand. It is also used in Australia (Robinson and Wheeler 1983; Williams *et al.* 1995). Spotlight counts are a rapid and simple assessment of rabbit abundance, allowing sampling over large distances and different habitat types (Williams *et al.* 1995). However, there is little information available on the factors that affect the precision of these counts. Weather conditions, season, and lunar illumination have been shown to affect the proportion of rabbits above ground at night (Allan 1993). It is not known how spotlight counts relate to absolute rabbit densities, or how precisely they can describe the percentage changes in rabbit densities following a poison operation.

Here we look at the variability in line-transect spotlight counts of rabbits. We calculate the resources required in terms of numbers of transects, nights and observers needed to provide spotlight counts of certain levels of precision. We describe the statistical relationship between spotlight counts and actual numbers of rabbits per hectare and the precision of spotlight counts for estimating percentage kill following a poison operation.

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Methods

We conducted our study on farmland in the Mackenzie Basin, South Island, New Zealand. Vegetation consisted primarily of one species of short tussock (*Festuca novaezelandiae*), pasture grasses, the rosette-form weed *Hieracium praeltum* and matagouri shrubs (*Discaria toumatou*). In total, 17 km (divided into two lines of 9 and 8 km) were marked with reflectorised stakes. Within each 1-km transect 1–3 100-m lengths (26 in total) were also marked. Seventeen of these were sited half way along each 1-km transect. The additional nine were sited to ensure that all vegetation types were assessed. Counts were made from a motorcycle travelling at *c*. 7 km h^{-1}. The observer wore a helmet-mounted 30-W spotlight that was swung in an arc 90° to each side of the direction of travel. The spotlight-beam provided visibility up to 50 m either side, but the observable distance depended upon topography and vegetation. At the end of each 1-km transect, records were made of the total number of rabbits seen, moon and weather conditions (arbitrary scales of wind, rain, cloud cover and snow). Separate counts were kept for the 100-m lengths and the full 1-km transects. A detailed map of the location and layout of the transects is presented by Moller *et al*. (1997).

Two observers each counted both lines once per night. The first counts started just after sunset and took 1.3 h. The second count began 1 h after the finish of the first count. The observers alternated the order in which they counted the lines. Counts were made on 11 nights between 12 and 31 August 1991.

After a week of non-toxic pre-feeding, poison baits (carrots with 0.02% 1080 poison) were laid on 7 September 1991. Rabbit carcasses were collected within 20 days from the surface and from underground burrows of 26 quadrats (marked 50 m to each side of the 100-m lengths marked in the pre-poison counts). The total number of surviving rabbits flushed from each quadrat during the searching was added to the dead count to give an estimate of the total rabbit density. The density of burrows was scored as low, medium or high.

A linear model was used to estimate the components of variability in log-transformed counts of rabbits (log-count) per 1-km transect attributable to the different factors (transect, observer, run, weather and night). Confidence limits for the variance components associated with the random factors (transect, observer and night) were calculated using the method described by Graybill (1961, pp. 370–373). Although the data are not balanced, the degree of imbalance is not large (number of nights varies from 16 to 21). The limits should therefore give a reasonable indication of the precision of the estimates.

The components of variability in log-count were used to predict the precision of any future spotlight counts, assuming only one run per night in fine weather. This analysis ignores the potential for temporal or spatial correlation in the error terms associated with the model. If these correlations are large and positive, the variance components (Table 1) will tend to be underestimated compared with those that would be obtained if all transects and nights were sufficiently spaced to be independent. In order to assess the robustness of our analysis to any such correlation, the residuals from the linear model were analysed in two ways. First, to assess the magnitude of any temporal correlation, each residual was paired with the residual on the same 1-km transect for the following night. A similar assessment was carried out for neighbouring 1-km transects: each residual was paired with the residual on the same night for the neighbouring transect. The overall correlations between these pairs of residuals were 0.02 (temporal) and 0.14 (spatial). The potential impact of this level of correlation on the variance components was gauged using results provided by Diggle (1990, pp. 90–91). These showed that the components might be underestimated by at most 5%, implying that the analysis is robust to this level of correlation.

In order to calibrate the counts in terms of actual rabbit densities, linear regression was used to model log-count per 100-m length in terms of the observed log-density per quadrat, having adjusted for any

Table 1. Sources of variation in spotlight counts of rabbits

Variance components (with lower and upper 90% confidence limits) were estimated from the linear model relating log-count per kilometre to transect, night, observer and weather effects

Component	Estimate	Lower	Upper	% of total
Transect	0.1221	0.0724	0.2472	53.8
Night	0.0141	0.0064	0.0354	6.2
Observer	0.0039	0.0007	0.0102	1.7
Residual	0.0870	0.0764	0.1001	38.3

differential weather, night and observer effects. Inverse prediction (Williams 1959) was used on the resulting regression line to determine the precision of both the predicted density and the predicted change in density following poisoning. Log-count per 100-m length was also modelled in terms of the effects of burrow density using logistic regression, with and without first accounting for the effects of log-density. The effects of terrain and vegetation on the visibility of a cardboard rabbit model (see Fletcher *et al.* 1995 for details) were included in the model. Details of the analyses and calibrations are given in the Appendix.

Results

Spotlight counts

Spotlight counts varied between 14 and 321 rabbits per kilometre, averaging 125.1 (s.d. = 56.2). Snow or heavy rain decreased the number of rabbits seen by an average of 25.1% ($F_{1,13}$ = 7.0, P = 0.02). The two observers varied in their counts along the 17 1-km transects by an average of 9.0% ($F_{1,299}$ = 8.4, P = 0.004). The first count of the night produced on average 11.9% more rabbits than the second count ($F_{1,299}$ = 14.3, P = 0.0002). Stage of the moon and cloud cover were confounded with other weather conditions so that it was not possible to determine their effects. Rabbit counts per 100-m length increased with burrow density ($F_{2,23}$ = 4.7, P = 0.019) (Fig. 1).

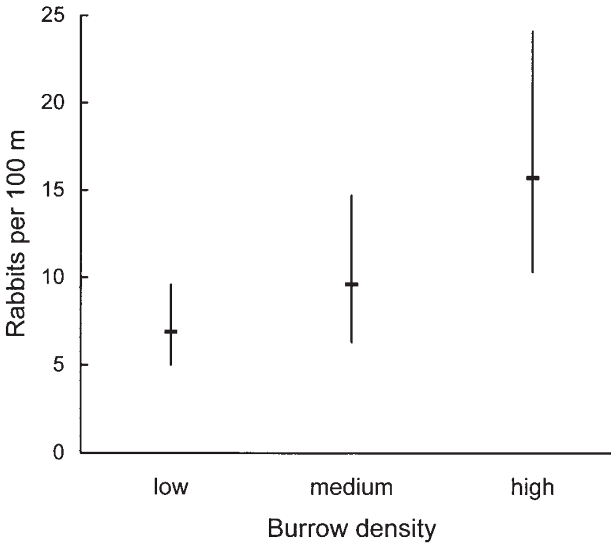

Fig. 1. Variation with burrow density in (back-transformed) mean number of rabbits (±95% CI) counted by spotlight per 100-m length.

Variability in spotlight counts occurred primarily between 1-km transects, followed by residual (unknown) sources, then night and observer (Table 1). To approach 5–28% precision in the spotlight counts as estimators of rabbit abundance, large numbers of transects, nights or observers would be required (Table 2). Using practical levels of resources (25 km, <6 nights) would achieve precision of between 12–20% and 13–26%.

Post-poison assessment and count calibration

The total number of rabbits found per quadrat after the poison operation was 2–52 (mean = 19.4). Overall, 93% of the rabbits on the quadrats died (n = 504). There was a significant ($F_{1,24}$ = 16.8, P = 0.0004) but weak relationship between the post-poison assessment of actual rabbit density and average spotlight counts per 100-m length (Fig. 2). The calculated accuracy of the spotlight counts as estimates of actual rabbits per hectare was low, especially at high mean counts

Table 2. Numbers of transects, nights and observers required to provide different levels of precision in the relative rabbit abundance index

Precision is defined as the difference between the estimated abundance and the lower or upper confidence interval, expressed as a percentage of the estimate. Methods for determining the ranges of the confidence limits are described in the Appendix

Transects	Nights	Observers	Precision based on Lower 95% CL	Precision based on Upper 95% CL
1000	5	1	5–28%	6–39%
25	1000	1	9–29%	10–41%
25	5	1000	12–20%	13–26%
25	5	1	13–30%	15–43%
25	4	1	14–31%	16–44%
25	3	1	14–31%	17–45%
25	2	1	16–32%	19–47%
25	1	1	19–36%	23–56%

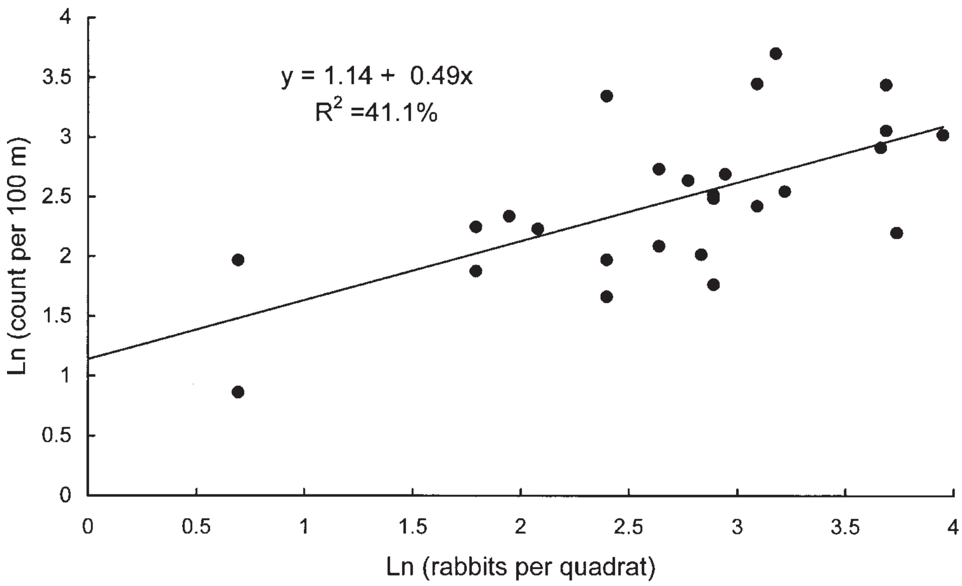

Fig. 2. Relationship between the number of rabbits counted per 100-m length and the estimate of actual rabbit density. Data are ln-transformed.

(Table 3). The slope of the log-log regression line was significantly different from unity (t_{24} = 4.2, P = 0.0003), indicating that the relationship was not linear. Thus, the percentage change in rabbit counts cannot be used directly to describe percentage changes in actual rabbit density.

The change in counts before and after a poison operation can be precise, but only at high kill rates (Fig. 3). If the change in spotlight counts is 80% then the actual kill is likely to be greater than 78–87% (Table 4). But at a low percentage spotlight count change, e.g. 60%, the actual kill could vary widely. Precision of estimates of poisoning efficacy increases with the number of counts that are made before and after the poisoning. However, this improvement is slight, especially when efficacy is high.

Table 3. Density of rabbits predicted from the mean count per kilometre, for one observer counting 25 1-km transects on each of five nights
The estimated density and confidence limits are based on the calibration involving log-count per 100-m length and log-density. Methods for determining the ranges of the confidence limits are described in the Appendix

Observed mean count per km	Estimate	Estimated rabbits per hectare Lower 95% CL	Upper 95% CL
0	0	0	0
30	1	0	2–3
60	3	0–1	7–10
90	8	2–3	14–24
120	14	4–7	26–48
150	21	6–12	48–89
180	31	10–17	89–153
210	42	14–22	153–250
240	55	18–28	247–390
270	70	22–34	382–582
300	87	27–40	566–840

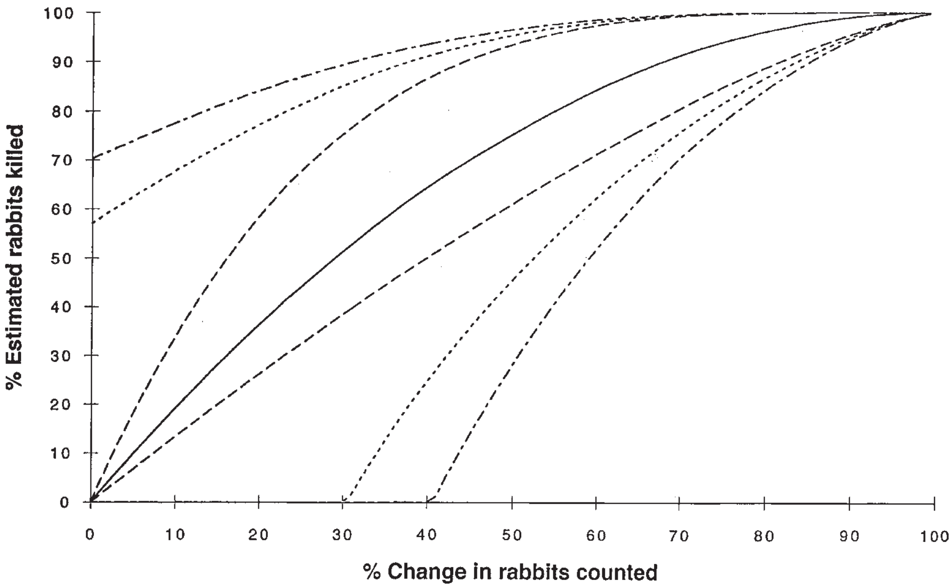

Fig. 3. Estimated percentage reduction in rabbits per ha as determined from the percentage change in spotlight counts of rabbits before and after poisoning. Upper and lower 95% confidence intervals are given for 25 quadrats with two counts before and after poisoning (— - —), 100 quadrats with five before and after counts (- - -) and unlimited resources (— — —).

Discussion

Reliability of the statistical models

The reliability of the 95% confidence intervals calculated in this study depends upon the accuracy of the counts of rabbits per 1-ha quadrat after the poison operation as indicators of the number of active rabbits on the transects during the preceding nights. This reliability can be

Table 4. Precision of the estimated change in rabbit numbers after a poison operation
Confidence limits are provided for both the percentage change in the spotlight counts and the estimated percentage change in rabbit density. Estimates are for (a) two nights before and two nights after poisoning, and (b) five nights before and five nights after poisoning, for a single observer counting 25 1-km transects. Methods for determining the ranges of the confidence limits are described in the Appendix

Count frequency	Observed reduction in counts	95% confidence limits			
		Spotlight counts		Quadrat density	
		Lower	Upper	Lower	Upper
(a) 2 nights	40	0–29	49–64	0–25	91–96
	60	33–53	66–76	21–63	98–99
	80	67–76	83–88	78–87	100
	90	83–88	92–94	93–95	100
	95	92–94	96–97	97–98	100
	99	98–99	99	100	100
(b) 5 nights	40	5–34	46–62	0–31	90–96
	60	36–56	64–75	26–65	98–99
	80	68–78	82–87	79–87	100
	90	84–89	91–94	93–95	100
	95	92–94	95–97	98	100
	99	98–99	99	100	100

inferred from all of the following facts. There was an appropriate interval between the spotlight counts and the extraction of dead rabbits, long enough to ensure that all that were going to die had done so (Oliver *et al.* 1982) but not so long that there would have been much recruitment to the rabbit population during that time of year (Robertshaw 1992). Robinson and Wheeler (1983) recorded very little reinfestation of rabbits within 20 days of conventional 1080 operations. Reinfestation during our study was especially unlikely as a severe winter reduced the survival of young rabbits in the Mackenzie Basin that year (J. D. Robertshaw and R. G. Mills, unpublished data). The size of the quadrats was appropriate to the distance over which the observers can detect both live rabbits and cardboard rabbit models (Fletcher *et al*. 1995). Night-time home ranges of rabbits are approximately 1 ha, or even less at high density (Gibb *et al.* 1978). Visibility obstructions did not significantly influence the spotlight counts (Fletcher *et al*. 1995). There was a high percentage kill, giving a robust estimate of the number of rabbits living in the area. Finally, the number of rabbits both counted at night and found on the quadrats increased with burrow density (Fig. 1 and Moller *et al*. 1997). Rabbits can die within 1 h of being poisoned by 1080 (McIlroy 1982), and almost all die within 24 h (Robinson and Wheeler 1983). They typically continue feeding until they collapse (Meldrum and Rowley 1957), suggesting that the rabbits did not move long distances to die in burrows.

Only 2 of the 26 quadrats had fewer than five rabbits per hectare. The statistical models may not be reliable at estimating very low rabbit densities.

Count variability and precision

The variability in counts between the first and second run may have been because rabbits may become less active after an initial feeding period just after dusk. It was unlikely to be because rabbits were scared underground or to other feeding areas during the first run (Williams *et al.* 1964). The effects of snow and heavy rain on our counts are consistent with observations of depressed rabbit activity in these conditions (Gibb *et al.* 1978; Cowan 1991). While we could not determine the effects of the stage of the moon or percentage cloud cover these variables may affect count indices of abundance. Villafuerte *et al*. (1993) found that rabbit activity increased on moonlit nights and decreased with increasing wind. Our results could also be explained by reduced detectability of rabbits in inclement weather. This effect may be even larger in areas with more diverse topography and vegetation than on our relatively flat and denuded study area except that terrain and vegetation had little effect on visibility (Fletcher *et al*. 1995). This is presumably because rabbits run as the motorcycle approaches and are noticed by the observer.

The potential for bias caused by the effects of weather and run can be minimised by counting only in good weather and for only one run per night, preferably just after dark when most rabbits are active (Williams *et al.* 1995). The variability between observers is relatively small, suggesting that there is little to gain from using more than one observer to attain a more accurate estimate of mean count. Correspondingly, it suggests that several observers can be used to increase the total number of transects counted without fear of introducing a large new variable. The greatest variability occurred from place to place and this will set bounds on the precision that can be achieved in the counts. It emphasises the need to fix exactly the path of the transect lines used before and after a poison operation or used for tracking a population through time. It also limits the value of spotlight counts as a relative index of rabbit abundance for comparisons between geographical areas. If counts are carefully fixed in space, they can be an effective way of indexing changes over time (Moller *et al.* 1996).

No matter what the precision of the counts, the wide confidence intervals for the predicted absolute abundance show that spotlight counts provide an inaccurate estimate of actual rabbit densities. At best, they may detect major regional differences in actual abundance spanning an order of magnitude or more.

Measuring poisoning efficacy

The repeated counts along the same transect before and after poisoning gave reasonably narrow confidence intervals for observed reductions in the counts above 80%. Clearly, the method is very useful for monitoring efficiency of poison kills at the levels normally achieved in control operations (Norbury and McGlinchy 1996). It will estimate RCD impacts provided that reductions of more than 80% are achieved. However, the confidence intervals may still be too wide to allow an accurate assessment of the speed at which a rabbit population will return to an economic injury level after a control operation. The much tighter confidence intervals on estimates of percentage kill (at high kill rates at least) emphasise the need to standardise observers and allow for differences in weather between the before and after counts on fixed transects. A slight difference in count caused by these variables will have a correspondingly large influence on estimated percentage kill.

The average rabbit spotlight count of 125 km^{-1} indicated that the study area had a high rabbit density (Norbury and McGlinchy 1996). The reduction in precision of the counts at high densities may have been caused by the observers' inability to count all individuals at such high density: Robinson and Wheeler (1983) demonstrated that a lower proportion of radio-tracked rabbits were recorded in spotlight counts when rabbit densities were high. Another possible cause is that rabbits flushed by the observer may trigger others to flight or to crouch for cover well in advance of where they can be seen. More advance warning from other rabbits may occur at high density so that the proportion counted would decline at high density.

Whatever the reason for the 'saturation' of the count, it has important implications for the estimates of poisoning efficacy. A given decline in the spotlight counts is likely to indicate a much higher decline in real abundance. Thus, poisoning efficacy can be much greater than the counts indicate. Suspected cases of neophobia (e.g. Oliver *et al.* 1982) may in fact be simply the result of chance imprecise counts. The lack of a linear relationship between spotlight counts and true rabbit abundance, as illustrated here, will also affect the precision with which one can assess the interactions between rabbit and predator population densities or impacts on alternative prey (Norbury and McGlinchy 1996). Our calibration technique allows spotlight counts to be used to assess these potential predator–prey interactions more precisely.

Conclusions

The spatial and unexplained variability in spotlight counts of rabbits make them an imprecise index of relative abundance. At practical levels of effort, spotlight counts cannot provide an accurate estimate of actual rabbit densities, especially when these densities are high. In poison operations to control rabbit numbers, before and after counts along carefully fixed transect lines can provide a more accurate estimate of percentage kill, but only when that kill is greater than 80%. Observed reduction in spotlight counts is likely to underestimate reduction in actual density because the spotlight count index 'saturates' at high rabbit density.

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Appendix

Precision of spotlight counts

Consider a spotlight survey involving p observers, each doing one run per night for n nights over s transects. We assume that all counts are made under good weather conditions, and that the log-count on transect i, night j by observer k can be modelled as

$$y_{ijk} = \tau_i + n_j + o_k + \epsilon_{ijk} \tag{1}$$

where τ_i, n_j and o_k are the effects of transect, night and observer respectively. All terms in the model are assumed to be random and uncorrelated, with variances σ^2_τ, σ^2_n, σ^2_O and σ^2 respectively.

The mean log-count can be written as

$$\bar{y} = \bar{\tau} + \bar{n} + \bar{o} + \bar{\epsilon}.$$

The $\bar{\tau}$ term measures the mean log-count over all transects. Its back-transformed value, exp($\bar{\tau}$), is taken to be an index of rabbit abundance. An unbiased estimate of $\bar{\tau}$ is $\bar{y}$, and 95% confidence limits for exp($\bar{\tau}$) are therefore given by

$$\exp\{\bar{y} \pm 2\sqrt{V}\}$$

where

$$V = \frac{\sigma^2_\tau}{s} + \frac{\sigma^2_o}{p} + \frac{\sigma^2_n}{n} + \frac{\sigma^2}{snp}$$

Estimates of the variances needed to predict these limits are given in Table A1.

Precision of density estimate

To consider the precision of the spotlight count as a predictor of actual rabbit density, τ_i in (1) is modelled as a linear function of the log-density, and so

$$y_{ijk} = a + bx_i + e_i + n_j + o_k + \epsilon_{ijk}$$

where a and b are parameters and x_i is the log-density in the quadrat(s) associated with transect i. The term e_i represents non-linearity in the relationship between τ_i and x_i, and has variance σ^2_o.

Table A1. Parameter estimates used to assess precision of spotlight counts for both 100-m and 1-km transects

The parameters σ^2_τ, σ^2_n, σ^2_O, and σ^2 were estimated from a linear model relating log-count to transect, night, observer and weather effects. The calibration parameters a, b, σ^2_b and σ^2_o were estimated by predicting what the mean log-count per transect would have been if all counts had been made in good weather, and regressing this against the log-density observed in the 1-ha quadrats. The mean of this log-density over all quadrats in the study is $\bar{x}$

Parameter	100-m counts	1-km counts
σ^2_τ	0.379	0.122
σ^2_n	0.017	0.014
σ^2_O	0.010	0.004
σ^2	0.269	0.087
a	1.200	4.128
b	0.493	0.238
σ^2_b	0.014	0.009
σ^2_e	0.253	0.098
$\bar{x}$	2.692	2.680

Note that in using this model, we are considering the spotlight count as a predictor of the density that would be observed in a 1-ha quadrat in the centre of the transect after a poisoning event similar to the one used in this study. This approach is more realistic than trying to predict the 'true' density for the area around each transect, and avoids the need to allow for any error in x_i as an estimate of 'true' density. In particular, simple regression techniques can be used to estimate a and b.

We are interested in estimating the back-transformed mean log-density, exp($\bar{x}$). The mean log-count can be written as

$$\bar{y} = a + b\bar{x} + \bar{e} + \bar{n} + \bar{o} + \bar{\epsilon}.$$

An obvious estimate of $\bar{x}$ is $(\bar{y} - \hat{a})/\hat{b}$, and 95% confidence limits for exp($\bar{x}$) are found using inverse prediction (Williams 1959). These are

$$\exp\left(\frac{-B \pm \sqrt{B^2 - 4AC}}{2A}\right)$$

where

$$A = b^2 - 4\sigma_b^2 \qquad B = 2[4\bar{x}\sigma_b^2 - b^2\bar{x}]$$
$$C = (b\bar{x})^2 - 4\left[\frac{\sigma_e^2}{17} + \bar{x}^2\sigma_b^2 + \frac{\sigma_e^2}{s} + \frac{\sigma_n^2}{n} + \frac{\sigma_o^2}{p} + \frac{\sigma^2}{snp}\right]$$

Estimates of the terms needed to predict these limits are given in Table A1.

Percentage reduction following poisoning

The change in mean log-count between two identical spotlight surveys can be modelled as

$$\bar{y}_{AB} = \bar{\tau}_{AB} + \bar{n}_{AB} + \bar{o}_{AB} + \bar{\epsilon}_{AB}$$

where, for example, $\bar{y}_{AB} = \bar{y}_A - \bar{y}_B$, and the subscripts represent before and after poisoning. An estimate of the percentage change in the abundance index is 1–exp ($\bar{y}_{AB}$), and 95% confidence limits are

$$1 - \exp\{\bar{y}_{AB} \pm 2\sqrt{V_{AB}}\},$$

where

$$V_{AB} = \frac{2}{s}(1 - \rho_\tau)\sigma_\tau^2 + \frac{2}{p}\sigma_o^2 + \frac{2}{n}\left(\sigma_n^2 + \frac{\sigma^2}{sp}\right).$$

and ρ_τ is the correlation between τ_{iA} and τ_{iB} This correlation has been assumed to be 1, but our conclusions are robust to this assumption.

By analogy with the case of a single survey

$$\bar{y}_{AB} = b\bar{x}_{AB} + \bar{e}_{AB} + \bar{n}_{AB} + \bar{o}_{AB} + d_{AB}w + \bar{\epsilon}_{AB}$$

and so 95% confidence limits for the percentage change in density are found by inverse prediction to be

$$1 - \exp\left(\frac{-B \pm \sqrt{B^2 - 4AC}}{2A}\right)$$

where

$$A = b^2 - 4\sigma_b^2 \qquad B = -2b^2\bar{x}_{AB}$$
$$C = (b\bar{x}_{AB})^2 - 4\left[\frac{2}{s}(1 - \rho_\eta)\sigma_e^2 + \frac{2}{p}\sigma_o^2 + \frac{2}{n}\left(\sigma_n^2 + \frac{\sigma^2}{sp}\right)\right]$$

Estimates of the terms needed to predict these limits are given in Table A1.

Predicting the precision of future surveys

In order to allow for the uncertainty associated with the estimates of the variance components in Table A1, the equations given above for predicting the 95% confidence limits to be expected in a future survey were used repeatedly as follows. For each variance component, an alternative estimate was selected at random from a distribution and used to predict the lower and upper 95% confidence limits concerned. This was repeated 1000 times, and the range of the middle 95% of the resulting predictions was recorded. The method used to generate each variance component was based on the assumption that the mean squares in the linear model analysis relating log-count to transect, night, observer and weather effects had independent distributions that were multiples of Chi-squared distributions (Graybill 1961, p. 370). This assumption was reasonable as the data were close to being balanced and the error terms were approximately normally distributed.