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Developing a census method based on sight counts to estimate rabbit (*Oryctolagus cuniculus*) numbers

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Abstract. A rabbit-census method, based on systematic counts conducted at night or at dawn and dusk, was developed and validated in terms of estimating the total number of rabbits present in a given area. Initially, models were developed under semi-natural conditions to describe the relationships between the numbers of rabbits counted and population size. Confidence limits were also calculated. The models were developed by comparing rabbit counts with the actual number of rabbits present, from a known population of animals. Only spotlight counts at night were considered reliable enough to estimate rabbit population size. During the autumn and winter months these represented ~60% of the population present. The model was subsequently validated, in two different exercises, following a series of field trials conducted under a variety of conditions on commercial farms. Initially, population estimates derived from the model were compared with those calculated using an alternative census technique. Population estimates, using the two techniques, were very similar at nine of the ten study sites. A second validation exercise was also conducted whereby the number of rabbits removed at each of the sites was compared with the difference between the mean pre- and post-removal spotlight counts. The results further supported the proposition that spotlight counts represent ~60% of the population present, with the difference between the two mean spotlight counts representing 61.2% (± 11.0, s.d.) of the number of rabbits removed. The census method therefore shows considerable promise as a means to estimate rabbit numbers under a range of agricultural conditions and therefore has the potential to predict accurately the economic costs of rabbit damage and also to gauge the effectiveness of various methods of rabbit control.

Introduction

The European rabbit (*Oryctolagus cuniculus*) is an environmental and agricultural pest of almost unrivalled potential (Thompson and King 1994). Where present, it is often associated with crop damage, the loss of valuable food resources to livestock, the depletion of native vegetation and the aggravation of soil erosion (e.g. Thompson 1994; Gibb and Williams 1994; Williams *et al.* 1995). In Britain alone, rabbits are responsible for economic losses to agricultural, horticultural and forestry interests estimated to cost farmers over £100 million annually (Rees *et al.* 1985).

Rabbit numbers are increasing in Britain following a dramatic decline after the introduction of myxomatosis. While myxomatosis is still prevalent in many areas, mortality during such outbreaks has fallen due to attenuation of the myxoma virus (Ross and Tittensor 1986) and increased levels of genetic resistance (Ross 1982; Ross and Sanders 1984). The total pre-breeding population is currently estimated to be more than 37 million (Harris *et al.* 1995) and given that the carrying capacity for rabbits has yet to be reached in many areas (Trout *et al.* 1986) further population increases are to be expected.

Problems caused by rabbits in Britain are therefore likely to worsen and research is currently being conducted to relate the extent of problems, such as crop loss, to the size of rabbit populations (e.g. McKillop *et al.* 1996). This information is essential to any cost–benefit analyses of management strategies and therefore of great importance to both growers and Government advisers interested in the impact of rabbits on agriculture. The provision of sound advice on the cost-effectiveness of rabbit-management strategies therefore requires the development of a simple and reliable means to estimate the number of rabbits present in a given area and hence the extent of the problem.

Despite the need for reliable estimates of population numbers, their derivation continues to prove difficult (Putman 1984). Most of the techniques devised to assess the numbers of individuals in free-ranging mammalian populations demand a great deal of time and effort (Taylor and Williams 1956; Wilson and Delahay 2001) and usually

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provide only an index of relative abundance rather than an estimate of actual numbers (Diaz 1998). More valuable would be a means to quickly and reliably estimate population size by calibrating indices of rabbit abundance. The provision of such a method would enable the information on crop yield losses arising from rabbit damage to be used most effectively by evaluating the cost-effectiveness of various management strategies. It would also allow landowners and occupiers to target areas in most need of control.

A number of indices have been used to assess the sizes of rabbit populations though few of them have been validated in the field (Williams *et al.* 1995). The techniques used presently range from direct methods such as trapping (Dunnet 1957*a*; Edwards and Eberhardt 1967) to indirect methods whereby various signs of rabbit activity are used to indicate presence or estimate abundance. Indirect methods are particularly useful for nocturnal or elusive species such as the rabbit. The rabbit signs most commonly used to estimate abundance are droppings (Taylor and Williams 1956; Wood 1988; Velazquez 1994) and burrows (Myers *et al.* 1975; Parer 1982; Parer and Wood 1986). More usually, however, rabbit numbers are assessed by counting them, either at night using a spotlight or at dawn and dusk. This technique has been used extensively in Australia and New Zealand (Dunnet 1957*b*; Myers 1957; Parer and Price 1987; Moller *et al.* 1996; Twigg *et al.* 1998; Fletcher *et al.* 1999) and, to a lesser extent, in Britain (Trout *et al.* 1986; Diaz 1998). Unfortunately, the technique gives only a snapshot assessment (i.e. the number of animals in a particular area and at a particular time). It does not take into account how many rabbits are on the field but are not seen or how many others that use the area are absent at the time the count is conducted. By measuring the relationship between the number of rabbits observed and the actual population size it may be possible to extrapolate from sight counts and provide reliable estimates of rabbit numbers.

Similar research has been conducted previously in Australia (Parer and Price 1987) and New Zealand (Fletcher *et al.* 1999) but, to date, no comparable work has been done in the very different setting of lowland agriculture in Britain. The primary aim of this study was thus to develop and validate, in Britain, a rabbit-census method based on a series of systematic counts conducted either at night using a spotlight or at dawn and dusk. The precision of the technique would also be assessed to ensure that both growers and advisers could make reliable assessments of rabbit problems in the field.

Materials and Methods

The study was divided into two separate phases. The first aimed to develop simple models to describe the relationships between the number of rabbits counted (spotlight/dawn/dusk) and the size of the population present. Confidence limits were also calculated for these counts. The second aimed to assess the validity of these models under a range of agricultural conditions.

Developing the models

The initial phase of the study was conducted under semi-natural conditions in Hampshire (southern England). Twenty wild rabbits were trapped (10 male and 10 female), fitted with individually identifiable passive integrated transponders and introduced into a 1-ha rabbit-proof enclosure. The enclosure consisted of a grass field (0.75 ha) and an adjoining woodland harbourage (0.25 ha). A wire fence separated the two areas and rabbit access into the field was possible only through five ground-level tunnels in which transponder detectors were placed. This automatic monitoring system was able to record when tagged individuals left and returned to the harbourage and thus enabled the number of rabbits present on the field at any one time to be calculated.

After a short acclimatisation period (two weeks), during which the rabbits became familiar with their new environment and began to regularly use the tunnels, the monitoring system was activated and data were collected on the movements of the tagged rabbits over a six-month period (October–March). During the same period, two spotlight counts and two sets of dawn/dusk counts were conducted each week. Spotlight and dusk counts were not conducted on the same night to avoid disturbance of the population before spotlight counts. The night counts were conducted approximately 1 h after sunset using a halogen spotlight (one million candlepower). Dawn and dusk counts were conducted using hand-held 10×40 binoculars, at sunrise and approximately 1 h before sunset respectively. All the counts were made from a pre-determined fixed transect that enabled complete coverage of the study field with minimal disturbance to the rabbits. The data were analysed to develop simple models to describe the relationships between the numbers of rabbits counted, the actual numbers present on the field at the time of the count and the total population using the field.

Thirty-seven counts were made at dawn, dusk and at night, and a Monte Carlo approach taken (sampling from the actual distribution with replacement) to determine the 95% confidence limits of the population prediction for increasing numbers of counts. As the number of individual counts increases, the variance in the data decreases, and thus the confidence limits converge towards the mean. The 95% confidence limits were calculated as two standard deviations from the mean.

Validating the models

The second phase of the study was conducted over two years, between September and March of 1999–2000 and 2000–01, on commercial farms in North Yorkshire (northern England). The aim was to compare and further assess, in field trials, the validity of the predictive models under a variety of agricultural conditions. Ten trials were conducted, each lasting four weeks and consisting of a series of rabbit counts before and after a proportion of the rabbits was removed.

Six sites were selected during the first year (all pasture) and four in the second (two cereal, one set-aside and one stubble). All had a history of rabbit damage. At each site, six spotlight counts and six sets of dawn/dusk counts were conducted over a two-week period. Mean rabbit counts and standard deviations, for each of the three count types, were derived from the mean counts for each trial. The estimated uncertainty in the proportion of rabbits seen at each site was also calculated, i.e. the 95% confidence limits derived from the earlier models (based on six counts being conducted).

Spotlight counts took place 1 h after sunset using a spotlight (one million candlepower). Dawn counts took place at sunrise and dusk counts 1 h before sunset (both using 10×40 binoculars). Where possible, counts were made from a pre-determined position within each of the fields from which the whole area could be surveyed for the presence of rabbits. If the whole of the study area could not be viewed using this technique a fixed transect was walked to cover the whole site. Counts were made only on nights during which visibility was good, and thus foggy, misty and heavy rain conditions were avoided. Extremely bright nights or windy conditions were similarly avoided. Data collected during this period were incorporated into the models and extrapolated to estimate the size of the rabbit population at each site.

Following this first series of counts, a known number of rabbits (~75% of the maximum number counted) were removed from each site by either cage trapping or ferreting and counts conducted, as before, for a further two weeks. This provided a second estimate of the size of the original rabbit population and the difference between the mean counts before and after the removal of rabbits determined what proportion of the population was removed and hence, by extrapolation, the size of the original population. Provided a high proportion of the animals was removed, and assuming that the proportion of rabbits counted before and after remained at a similar level this method should satisfactorily estimate population size (Taylor and Williams 1956). Comparison of the two estimates offers a test of the validity of the predictive model based on the data from the enclosure study.

A second validation exercise was also conducted whereby the number of rabbits removed from each of the sites was compared with the difference between the mean pre- and post-removal counts. Further validation would be provided if the difference between the two means represented the same percentage of the number of rabbits removed as the proportion of the total population observed during the counts, as determined by the models. For example, if 10 rabbits were removed the difference between the pre- and post-removal counts could range from 10 (if the model predicts that counts represent 100% of the total population) to zero (if the model predicts that counts represent 0% of the total population). In reality, the figure is likely to fall somewhere between these two extremes.

Results

Developing the models

Results from the initial phase of the study indicated that the highest proportion of rabbits (60%) was observed at night, using a spotlight (Fig. 1). The counts at night (12.1 ± 3.24, mean ± s.d.) did not differ from the numbers of rabbits present on the field at the time of the count as indicated by the automatic monitoring system (13.0 ± 3.52, mean ± s.d.). A plot of the individual spotlight rabbit counts against actual numbers is presented in Fig. 2. The dawn (0.8 ± 0.97, s.d.) and dusk (5.2 ± 2.73, s.d.) counts were much lower (Fig. 1) and during these periods only a small proportion of the population was observed (dawn 4%; dusk 26%). Data from the automatic monitoring system also indicated that few rabbits are present above ground during these periods (dawn, 1.26 ± 1.54, mean ± s.d.; dusk, 6.48 ± 3.14, mean ± s.d.).

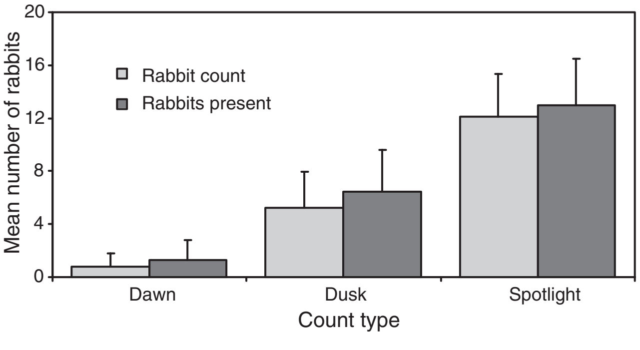

Fig. 1. The mean numbers of rabbits observed (± s.d.) and the actual numbers of rabbits present at the time of the dawn, dusk and spotlight counts (population size = 20).

In order to estimate the 95% confidence intervals for multiple counts, 2000 Monte Carlo simulations were performed, and the 2.5 and 97.5 percentiles were calculated around the mean (Table 1). Population estimates and confidence limits can be generated from this table by dividing the mean of *n* counts by the relevant values (see below for a worked example). For the dawn counts the 95% confidence limits include zero for up to six counts, thus no

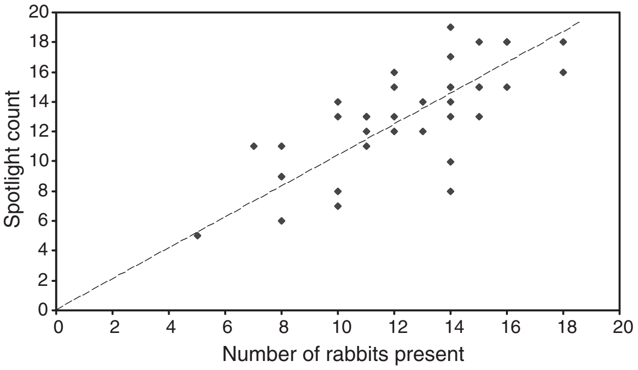

Fig. 2. The relationship between the spotlight rabbit counts and the actual numbers of rabbits present at the time of the counts, as indicated by the automatic monitoring system. A point would lie on the broken diagonal (line of equality) if the number of rabbits counted and the number present were identical.

Table 1. The mean proportion of the rabbit population observed at dawn, dusk and at night (spotlight), and the 95% confidence limits for increasing numbers of counts (population size = 20)

Count type	Mean proportion observed	No. of counts	95% confidence limits
Dawn	0.036	1	0–0.126
		2	0–0.100
		3	0–0.088
		4	0–0.081
		5	0–0.076
		6	0–0.073
Dusk	0.261	1	0–0.5285
		2	0.073–0.449
		3	0.107–0.415
		4	0.128–0.394
		5	0.141–0.381
		6	0.152–0.370
Spotlight	0.605	1	0.285–0.925
		2	0.377–0.833
		3	0.418–0.792
		4	0.444–0.766
		5	0.460–0.750
		6	0.473–0.737
		7	0.483–0.727
		8	0.491–0.719
		9	0.497–0.713
		10	0.503–0.707

meaningful population estimate can be made (six counts gives a minimum population estimate of 10 rabbits). For the dusk counts, only the single count includes zero, and with six counts the 95% confidence limits are 14–34 rabbits. For the spotlight counts, no estimates include zero, and a single count gives confidence limits of 13–42 rabbits, and six counts gives confidence limits of 16–26 rabbits. The spotlight counts therefore give the tightest confidence limits. For example, if the mean of six spotlight counts was 15, then the population estimate would be 15/0.605 = 25 rabbits. Similarly, the lower 95% confidence limit would be 15/0.737 = 20 rabbits, and the upper limit would be 15/0.473 = 32 rabbits (see Table 1 for the relevant values). We have presented the data for 10 spotlight counts to allow confidence limits to be calculated.

Validating the models

Results from the first six field trials followed a similar pattern to those from the initial phase where rabbits were housed under semi-natural conditions. Pre-removal counts indicated that most rabbits were observed at night (22.4 ± 8.39, mean ± s.d.) and relatively few at dawn (2.3 ± 1.83, mean ± s.d.) and dusk (3.3 ± 3.74, mean ± s.d.). At this point, it was considered that dawn and dusk counts were too small and variable to be of any use in developing predictive models and the remaining four trials therefore concentrated on the spotlight counts. Consequently, validation was sought for the spotlight model only.

The model developed from the initial data indicated that spotlight counts represented ~60% of the total rabbit population. To validate this model, spotlight counts from the field trials were extrapolated to estimate the size of the rabbit population at each site. These figures were compared with population estimates calculated using a second, alternative, technique determined from the equation:

$$x = n/[1 - (c_2/c_1)],$$

where x is the estimated initial population size, n is the number of rabbits removed and c_1 and c_2 are the mean numbers seen during pre- and post-removal counts respectively. The relationship between these two estimates is presented in Fig. 3.

Pearson's correlation coefficient indicates a significant positive association between the population estimates, derived using the two techniques, at nine of the ten sites (Pearson's correlation: $r = 0.87$, $N = 9$, $P < 0.01$). At the other, where an outbreak of myxomatosis occurred, the model predicted a population size almost twice as large as the validation method and this site was therefore excluded from analysis. The small P value strongly suggests that the two population estimates are linearly related over the range of densities observed. It does not, however, measure the agreement between them. Perfect agreement would exist only if the data points in Fig. 3 lay along the line of equality (linear relationship, zero intercept, slope 1). The slopes and intercepts of the regression line for the field data and the line of equality do, in fact, appear to be very similar and at only one of the sites do the confidence limits for the data point not bound the theoretical values (Fig. 3). To measure the level of agreement, the differences between the two population estimates were plotted against their means and the 95% limits of agreement calculated from the mean difference ± 1.96 standard deviations (Fig. 4); 95% of differences should lie between these limits (Altman and Bland 1983; Bland and Altman 1986). All of the points on our graph fall between these limits, which suggests that there is no systematic bias and that errors fall within acceptable levels throughout the range measured.

The second validation method compared the number of rabbits removed from each site with the difference between the pre- and post-removal spotlight counts. Our model

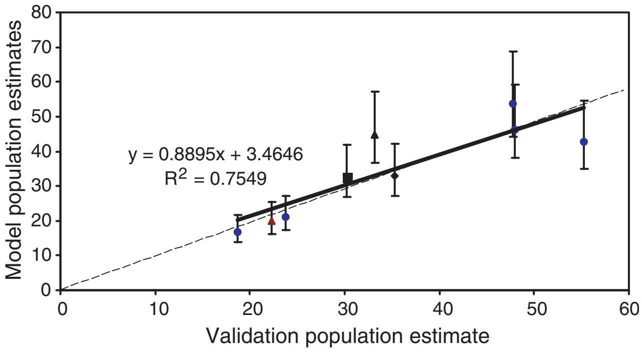

Fig. 3. The relationship between the mean validation population estimates and the model population estimates (mean ± 95% confidence limits from Table 1) for nine sites in northern England (●, pasture sites; ▲, cereal sites; ◆, set-aside site; ■, stubble site). The site where counts were affected by an outbreak of myxomatosis has been excluded. A point would lie on the broken diagonal (line of equality) if the validation population estimate and the model population estimate were identical.

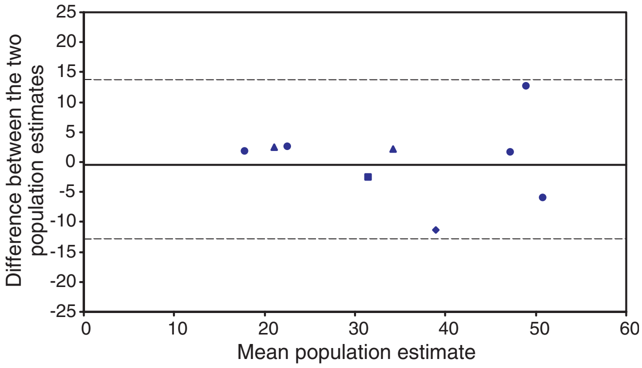

Fig. 4. The differences between the spotlight count population estimates and the validation population estimates against the mean population estimate (●, pasture sites; ▲, cereal sites; ◆, set-aside site; ■, stubble site). The broken horizontal lines represent the 95% limits of agreement and the solid horizontal the mean difference between the two population estimates.

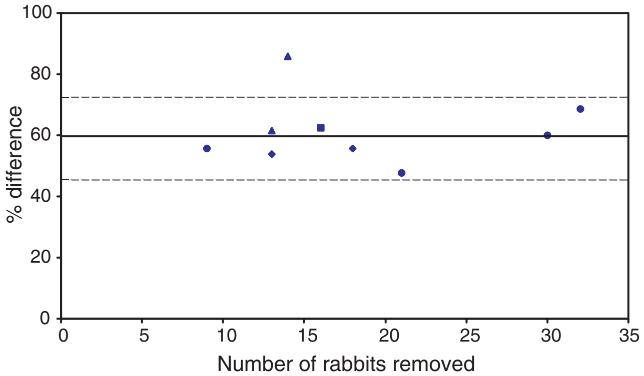

Fig. 5. The percentage differences between the number of rabbits removed at each of the sites and the difference between the mean pre- and post-removal spotlight counts (●, pasture sites; ▲, cereal sites; ◆, set-aside site; ■, stubble site). A point would lie on the solid horizontal line if the model holds true and spotlight counts represent 60% of the total population. The broken lines represent the 95% confidence limits around this line as determined during the development phase of the model (based on six counts being conducted).

predicts that the difference between the two mean counts should represent ~60% of the number of rabbits removed, i.e. 40% of the rabbits that were removed would not have been observed during the spotlight counts. This does appear to be the case and the difference between the counts, conducted at nine of the ten sites (the site where myxomatosis was prevalent was excluded from the analysis), represented, on average, 61.2% ± 11.0 (s.d.) of the number of rabbits removed. A plot of the individual percentage differences, for each of the test sites, is presented in Fig. 5. The results from all but one of the sites fall within the 95% confidence limits as determined, using Monte Carlo simulations, during the development phase of the model.

Discussion

Of the three types of visual count originally considered, only spotlight counts, which were conducted between October and March (autumn/winter in Britain), appeared to be large enough, and accurate enough, to provide reliable estimates of rabbit population sizes. Rabbit monitoring is most effectively conducted during this period for several reasons. First, plant height makes it possible to count rabbits. Spring and summer growth can often impair observations and differences in plant height between habitat types mean that reliable comparisons cannot be made (Barnes *et al.* 1983; Stoate and Tapper 1989). Second, overwintering numbers of rabbits are relatively stable whereas summer peaks can be highly variable (Tittensor 1981). Closed populations, where there is little birth, death, immigration or emigration, are best used when trying to determine population size (Slade and Blair 2000). Third, the winter months coincide with the period when landowners and occupiers are advised to conduct their control operations. Information regarding rabbit numbers is therefore most useful at this time of year.

The low numbers of rabbits observed at dawn and dusk may be linked to low levels of activity caused by disturbance, which can delay emergence, particularly during the winter months (Dunnet 1957*b*; Rowley 1957; Lord 1959; Kolb 1986). Variation in emergence times has been shown previously to be important in relation to the use of sight counts as a method of estimating rabbit abundance (Dunnet 1957*b*). During these months, therefore, dawn and dusk counts are likely to result in an underestimation of rabbit numbers and should be avoided. Lord (1963) suggested that sight counts should be conducted during the period of maximum daily activity. For rabbits, which are generally crepuscular and nocturnal in areas subjected to disturbance (Macdonald *et al.* 1998), this is at night (Lord 1959). Spotlight counts may therefore give a more accurate estimation of rabbit numbers because they generally avoid the problems associated with disturbance (Lord 1959).

Our model predicts that winter spotlight counts, conducted one hour after sunset, represent ~60% of the total rabbit population using the area (with 95% confidence limits of 47–74%). Field trials to validate this figure were encouraging, especially considering the range of agricultural conditions over which the model was tested. At nine of the ten field sites, population estimates derived using the model and those calculated using a second census method compared extremely well. At the other site, the relatively poor agreement between the two population estimates was explicable in terms of an outbreak of myxomatosis during the census period. This could have resulted in the low validation population estimate observed. The second validation exercise further supported the proposed model, thereby enhancing the argument for its use as a simple and reliable means to estimate rabbit numbers.

In a previous study, Parker *et al.* (1976) also found a significant agreement between estimated rabbit abundance and the total numbers of rabbits observed during spotlight counts. However, most previous research suggests that the proportion of the rabbit population seen during spotlight counts is highly variable and that counts should therefore be interpreted with caution and used only to compare relative abundance (Myers 1954, 1957; Taylor and Williams 1956; Dunnet 1957*b*; Myers and Schneider 1964; Fletcher *et al.* 1999). However, results from the present study are more robust than those previously reported and there may be a number of reasons for this.

Fundamental to any census method based on sight counts is the assumption that the counts are proportional to the population size. Almost all of the individuals present may be seen at some time but not all will be present at once (Smith and Nydegger 1985). It is therefore essential to conduct a series of counts to obtain a representative estimate of the proportion of total rabbits present. The best way to do this is to standardise conditions as far as possible (Macdonald *et al.* 1998). In our study this was achieved by avoiding extremes of weather which are known to affect activity and therefore the proportion of rabbits above ground (Newman 1959; Gibb *et al.* 1978; Cowan 1991; Thompson 1994; Moller *et al.* 1996). Bright moonlit nights, which can also affect activity (Kolb 1992; Villafuerte *et al.* 1993) and misty/foggy nights that might affect visibility, were similarly avoided. Observer bias may also change proportional relationships (Slade and Blair 2000) and this problem was avoided by conducting all the counts from either a pre-determined point within the study field or from along a fixed transect from which the whole of the field could be viewed using the spotlight. By conducting a series of counts over a relatively short period we also counteracted the problems associated with open populations and limited the confounding effects of varying conditions. We chose to conduct a series of six counts to get a representative proportion of the total populations with acceptable confidence limits. This number of counts fell between the three recommended by Trout and Tittensor (1989) and the 19 suggested by Moller *et al.* (1996). The results suggest that no more than six counts are required to provide sufficient precision for the technique. An additional four counts reduced the confidence limits by just 0.06%. We also standardised the time of the counts in relation to dusk and carried out counts only during autumn and winter when rabbit numbers in Britain are most stable. This combination of factors may go some way to explain the consistently accurate population estimates obtained during the study.

Overall, our results suggest that the census technique based on spotlight counts shows considerable potential as a robust means to estimate rabbit numbers under a range of British agricultural conditions. If, however, researchers in other countries wish to use the model to predict rabbit numbers we would recommend that further validation be conducted. The technique will work best in relatively small open areas and will be most representative of self-contained, aggregated populations of rabbits with little immigration or emigration. Provided measures are taken to standardise the counts, use of the technique will enable the size of rabbit populations in the field to be simply and reliably estimated. When combined with a population model and yield loss data this information will provide a valuable means by which to gauge the economic costs of damage and the cost-effectiveness of various management methods (Smith 2001). The census method will thus serve as a valuable tool in helping to resolve statutory and advisory issues relating to rabbit damage by enabling advisors to decide whether further action, in the form of more detailed investigations, is warranted on a case-by-case basis. The development of a suite of census methods offering varying degrees of resolution, appropriate for different levels of severity of the problem, would therefore serve as a useful tool to inform statutory and advisory services associated with resolving real rabbit-management issues.

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