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Abundance indices: reliability testing is crucial - a field case of wild rabbit *Oryctolagus cuniculus*

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We examined an index of abundance for rabbits *Oryctolagus cuniculus* involving a spotlight plot count (SPC) using capture-mark-resighting as a reference method in five study areas. In these areas, density varied over a wide range, from 0.7 to 23.4 rabbits/ha, which is representative of most European populations. The SPC precision was good, as the coefficient of variation ranged within 5-54%, the median value being 17%. We showed area and year effects on the index and a significant relationship between the SPC and ln(density) ($P < 0.0001$). The logarithmic relationship between density and SPC suggests a saturation of the index when density increases. Despite the fact that the SPC index was highly correlated with density, its ability to detect population changes was rather poor. This lack of sensitivity may be due to factors affecting rabbit detectability such as climatic conditions, lunar phases, observers, changes in crop rotation and, more generally, to factors affecting the number of rabbits above ground at the time of the count. The area effect means that the index is not suitable for comparing data recorded in different areas. The year effect is an actual obstacle to the use of this index since, within a defined area, the temporal changes in the index values are not related only to the estimated density. Our study highlights the necessity to validate abundance indices against reference methods so as to check their ability to detect changes in population size and their suitability for comparing data from different areas.

Key words: index of abundance, Oryctolagus cuniculus, reliability, spotlight plot count, study area effect, year effect

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Abundance indices are widely used in field studies of mammals because it is rarely possible to obtain an accurate estimate of the actual population size (Dice 1941, Thompson et al. 1998). However, some researchers have pointed out the danger that such indices may not accurately reflect population trends (Rotella & Ratti 1986, Eberhardt & Simmons 1987, Thompson et al. 1998) and, consequently, have suggested that population indices should be tested against other known methods. In practice, this means calibration against more accurate methods such as capture-mark-recapture (CMR) methods (Bayliss et al. 1986, Freeland 1986, Hutton & Woolhouse 1989). Such methods are widely used in research but are expensive and difficult to apply in wildlife management (Caughley 1977, Engeman 2003). Nevertheless, they give reliable estimates of the population size under some assumptions and, therefore, can be considered as reference methods.

In France, the wild European rabbit *Oryctolagus cuniculus* is an important game species. However, when abundant, it can become a pest responsible for significant damage to crops. This particular status, game but also a potential pest, must be taken into account when devising management rules for the development of game populations while avoiding agricultural damage. As rabbit management should be based on sound information on population levels, an abundance index that is either reliable or calibrated to actual population size is required to assess rabbit abundance.

The methods used to estimate rabbit abundance are divided into three groups. Indirect methods are faecal pellet counts (Taylor & Williams 1956, Gibb et al. 1969, Wood 1988, Iborra & Lumaret 1997) or counts of warren entrances (Parer 1982, Parer & Wood 1986). Direct methods are mainly daylight counts (Myers 1957, Parer & Price 1987, Moller et al. 1996), twilight transect counts (Tittensor 1979, Beltran 1991) and spotlight transect counts (Rogers 1979, King et al. 1983, Marchandeau & Gaudin 1994, Fletcher et al. 1999). Most of these methods give an index of abundance, but few of them have been calibrated against a reference method. Spotlight transect counts are the most widely used method to monitor rabbit populations, but their reliability remains poorly documented and is controversial. A study carried out in New Zealand determined the precision and accuracy of spotlight counts made from a motorcycle along transects in a flat and denuded study area (Fletcher et al. 1999), and the researchers concluded that "spotlight counts provide an inaccurate estimate of actual densities". However, a more recent study using modelling to estimate population growth rates and a different survey protocol, i.e. a single observer, a 150-W instead of a 30-W spotlight and a 4-wheel-drive vehicle instead of a motorbike, demonstrated the ability of transect spotlight counts to detect changes in rabbit abundance (Caley & Morley 2002). Whatever their reliability, spotlight counts carried out on large transects cannot be used in closed or semi-closed landscapes where hedges border roads or tracks and thus prevent the counting of many fields. Moreover, this method, which is used to monitor populations in large areas, is not really suitable for monitoring the patchy populations living on small areas that are representative of most management units in France. Finally, it is costly to apply since at least two operators are needed to make a count.

The aim of our study was to measure the reliability of an abundance index and to test it under different biogeographic conditions in order to determine whether or not it was suitable over a wide range of habitats. The spotlight plot count (SPC) is a cheaper method than the spotlight transect count commonly used in Australia and New Zealand, and is more suitable for monitoring populations living on small areas and in the closed or semi-closed landscapes that are the habitats of most French rabbit populations. We defined reliability as a combination of three components: the precision, the bias, i.e. the pattern of the relationship between the index and the population size, and the ability of the index to detect trends in the population. The study was carried out in January to estimate changes in the size of wild rabbit populations before reproduction, the emergence of the first juveniles occurring from mid-February onwards. The capture-mark-recapture method was used as a reference. The SPC is a count made at census points by only one observer moving on foot between these points.

Material and methods

Study areas

To be widely useful, any survey method must be robust enough to be applicable in a large range of habitats.

Accordingly, our study was carried out in five different study areas, each with its own habitat characteristics. Two of these areas, La Chevallerais and Cerizay, were managed for rabbit hunting, but during the study no hunting occurred.

La Chevallerais (1°40'W, 47°28'N) is located in western France (Loire-Atlantique). The landscape is a bocage, i.e. an open woodland dominated by pastures. Hedgerows occur on 0.50-0.80 m high slopes. The climate is oceanic. Mean annual rainfall is 790 mm and mean annual temperature is 11.7°C. The study was conducted in an area covering 17 ha. Cerizay (0°40'W, 46°49'N) is also situated in western France (Deux-Sèvres). It is also a bocage, but with mixed farming. The climate is oceanic with a continental influence. Mean annual rainfall is 780 mm and mean annual temperature is 11.1°C. This 110-ha study area is managed for rabbit hunting. A free-living population has been established in artificial warrens. The Donzère-Mondragon reserve (4°42'E, 44°26'N) is located in southeastern France (Drôme and Vaucluse). The climate is Mediterranean with a continental influence. Mean annual rainfall is 830 mm and mean annual temperature is 13.2°C. The 35-ha study area is a shrub-steppe. Lalinde (0°44'E, 44°50'N) is situated in southwestern France (Dordogne). The 59-ha study area is included in a 125-ha game reserve comprising forest (93 ha), crops (12 ha), pastures (12 ha) and fallow land (8 ha). The climate is oceanic with a continental influence. Mean annual rainfall is 840 mm and mean annual temperature is 11.8°C. The Chèvreloup arboretum (2°16'E, 48°40'N) is located close to Paris. It is a 200-ha park in which a 10-ha study area was defined. The climate is oceanic with a continental influence. Mean annual rainfall is 600 mm and mean annual temperature is 10.1°C.

Data collection

In each area, the study was conducted over three years from December 1993 to March 1996. Each year, rabbits were caught in December using ferrets *Mustela furo* and nets. Captures were organised in the central parts of the study areas to limit edge effects when estimating population density. Rabbits were sexed, weighed and marked with coloured ear tags (Top-Tag®; Rockall-France, Vitré, France) that also had Scotchlite® (3 M, Brownwood, Texas) markers for individual identification at night. Each rabbit was marked with one ear tag on each ear, both tags being covered with the same combination of colours. The aim of this double marking was to decrease the risk of bias due to tag losses. Afterwards, the rabbits were released into their warrens. The only method to determine the age of live rabbits is by the detection of the epiphyseal disks of the tibia, but it is not reliable for rabbits > 7 months old (Rogers 1982). Since most rabbits were > 7 months old when captured in December, they were all considered to be adults.

Population size was estimated by capture-mark-resighting (CMR) using a 'robust design' (Pollock et al. 1990). Resighting was conducted on foot at night using a 100-Watt quartz-halogen spotlight and binoculars to identify the marked rabbits. The study areas were searched entirely to flush the rabbits in order to detect marked and unmarked rabbits with equal probabilities. Data recording began one hour after dusk. We recorded all sightings of marked and unmarked rabbits. For each area and each year, three sampling periods were organised to obtain resighting data on previously captured rabbits. The first sampling operation was undertaken on the day after capture and marking; the following two were carried out five weeks later, in January, and then again five weeks later, in late February or early March. Within each resighting period we undertook three resighting sessions (Table 1), usually on consecutive evenings except when unfavourable weather, i.e. fog or heavy rain, was likely to affect the probability of resightings.

The spotlight counts were undertaken on grazed parts of the study areas, using a 100-Watt quartz-halogen spotlight and binoculars. Grazed parts were determined *a priori* as plots, i.e. fields with < 10 cm high vegetation, excluding bare soil. The area of each survey plot was determined from a map. Hence, the number of census plots and their surface area differed among the study areas. When possible, the counts were made in January during the week of the resighting sessions. They were usually repeated during three consecutive evenings (except when unfavourable weather, i.e. fog or heavy rain, occurred) and began one hour after dusk. All observed

Table 1. Capture-resighting experimental design used in this study. Resightings were organised in three primary sampling periods (j = 1, j = 2 and j = 3), each being made of three resighting sessions; t_i means time i.

Capture	Primary sampling period								
	j = 1			j = 2			j = 3		
	Resighting session			Resighting session			Resighting session		
	i = 1	i = 2	i = 3	i = 1	i = 2	i = 3	i = 1	i = 2	i = 3
t_0	t_1	t_2	t_3	t_4	t_5	t_6	t_7	t_8	t_9

rabbits, both the marked and unmarked ones, were counted in all the survey plots. The number of observed rabbits was divided by the area of the survey plot and expressed in terms of the number of rabbits/ha. Since the study was carried out after the hunting season had ended, hunting had no influence on the resighting data.

Estimation of population size

All rabbits were considered to be adults. CMR data were fitted to a Cormack-Jolly-Seber (CJS) model using the computer program JOLLY (Pollock et al. 1990). All the resighting sessions within a sampling period were pooled. A rabbit was considered as having been resighted in a sampling period if it was seen on at least one of the three nights on which observations were made (Pollock et al. 1990). Goodness-of-fit tests of the models were computed with the program RELEASE using the sum of TESTs 2 and 3 (Burnham et al. 1987, Lebreton et al. 1992). TEST 2 was used to test the goodness of fit of the model to the data and detects possible trap-dependence. TEST 3 tested heterogeneity in recapture histories (Burnham et al. 1987). Thereafter, a 'death and emigration' model (full CJS) was chosen to estimate the number of marked rabbits alive at the time of the resighting sessions. The JOLLY program computed the estimates of resighting rates 'p' and of the marked population size 'M' for each sampling period.

As the aim of our study was to compare the SPC index (SPCI) to the actual population size before reproduction, we focused on the population size estimated in January, i.e. during the second sampling period, the SPC being performed at this time. At this time, the size of each population (N) was estimated according to the data recorded for both marked and unmarked rabbits. The JOLLY program provided the estimation of the number of marked rabbits alive (M) in each population. The number of unmarked rabbits alive (U) was estimated assuming that both the total number of sightings per individual (H1) and the resighting probability 'p_j' (H2) were equal for marked and unmarked rabbits. The number of sightings of marked and unmarked rabbits, respectively, were $C_m = m_1 + m_2 + m_3$ and $C_u = u_1 + u_2 + u_3$ where m_i and u_i were the number of sightings of marked and unmarked rabbits seen during the i^{th} secondary session of resighting. These sighting frequencies were field data. Assumption H1 means that $S_m/C_m = S_u/C_u$ where S_m (field data) and S_u were the number of marked and unmarked different rabbits seen during a primary sampling period. Therefore, $S_u = C_u.S_m/C_m$. Assumption H2 means that $S_u = p.U$, where p is the capture probability given by the CJS model. Finally $U = S_u/p$ and the size of the population in January was $N = M + U$. N was then related to the size of the area to obtain an estimate of rabbit density (rabbits/ha).

Reliability of the spotlight plot count

The reliability of the SPC was estimated by both the precision of the index, the relationship between the index and the estimated density, and the ability of the index to detect changes in population size.

The precision of the SPC was estimated using the coefficient of variation of the three repetitions of the count (Thompson et al. 1998).

The data set was made up of 45 spotlight count records (5 areas × 3 years × 3 counts) yielding 15 population density estimates (5 areas × 3 years). To study the relationship between the counts and the density estimates, we used linear mixed-effects models that may include fixed as well as random factors and allow autocorrelation and/or heteroscedasticity of the residuals (Pinheiro & Bates 2000). The fixed part of the model was a variable expressing the density estimates, which might be either density or ln(density). Area and year effects were assumed to be random factors with the year factor nested within the area factor, to account for correlation between observations at the same site and in the same year for a given site. Plots of the residuals versus fitted values, explanatory variables and factors were used for graphical exploration of heteroscedasticity and choice of the way to take this into account. Models identical with respect to their fixed part, but differing in random factors and/or residual heteroscedasticity, were compared using Akaike's Information Criterion (AIC; Akaike 1973) as recommended for such analyses (Pinheiro & Bates 2000). The AIC value is the deviance of the model adjusted for its number of parameters k (AIC = DEV + 2k). The models having the lowest AIC or an AIC very close to this minimum, a difference of less than 2 or 3 (Burnham & Anderson 1998), are considered to be the closest to the best model and of equivalent value to represent the information contained in the data set. Finally, according to the principle of parsimony, the selected model was the simplest when several models had equivalent AIC. After the random structure of the model had been selected, the variable included in the fixed part of the model was finally tested with an F-test conditional on the estimates of the random parameters (Pinheiro & Bates 2000). All models were estimated with the REML method using the nlme library of the R package version 1.8.1. (Pinheiro & Bates 2000, R Development Core Team 2003).

Finally, we tested the capacity of the SPCI to detect local rabbit abundance variations over time as if we were in an actual situation of population monitoring with three

Table 2. Goodness-of-fit tests to Jolly-Seber model calculated for each data set (year*area) by use of the sum of TEST 2 and TEST 3 given by program RELEASE; df = degrees of freedom.

		TEST 2 + TEST 3		
Study area	Year	χ^2	df	P
Chèvreloup	1994	5.561	2	0.065
Cerizay	1994	0.000	2	1.000
Donzère	1994	0.500	2	0.771
La Chevallerais	1994	3.438	2	0.196
Lalinde	1994	0.000	2	1.000
Chèvreloup[1]	1995	0.000	1	1.000
Cerizay	1995	0.636	2	0.731
Donzère	1995	0.173	2	0.918
La Chevallerais[2]	1995	5.561	1	0.020
Lalinde[2]	1995	0.000	1	1.000
Chèvreloup[1]	1996	0.649	1	0.444
Cerizay	1996	6.221	2	0.460
Donzère	1996	4.102	2	0.128
La Chevallerais	1996	1.950	2	0.398
Lalinde	1996	0.000	2	1.000

[1] TEST 2 non-valid
[2] TEST 3 non-valid

annual measures of SPC. In this way, we compared the three SPC measures for each study area for successive years with Mann-Whitney U-tests at a $P = 0.10$ level, as the number of observations did not allow us to obtain a smaller α error.

Results

Estimation of the population size

The goodness-of-fit tests of the CJS model to the data (Table 2) failed to provide any evidence for trap dependence or heterogeneity in the recapture histories when both TESTs 2 and 3 were valid. We can therefore assume that the CJS model fitted the data. Some tests were not valid due to sparse data. One may notice that for La Chevallerais 1995, TEST 2 was significant suggesting trap-dependence, but the sum of TESTs 2 and 3 could not be calculated because TEST 3 was not valid. On this basis, we calculated the rabbit population size and converted it to density according to differences in the size of each study area. The data indicate a wide range of rabbit population densities that varied from 0.7 rabbits/ha at Lalinde in 1996 to 23.4 rabbits/ha at Chèvreloup in 1994.

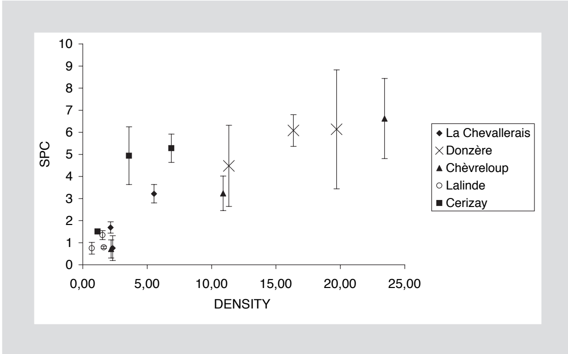

Figure 1. Relationship between SPCI (± 95% confidence interval) and density estimated by CMR for each study site. Both SPCI and estimated density are expressed as number of rabbits/ha.

Modelling of the relationship between SPCI and density

The SPCIs often gave convergent results within each year and for each area, with a coefficient of variation ranging within 5-54% (median value: 17%; Fig. 1).

After fitting the most complete models with either density or its logarithm as explanatory variable, plots of residuals versus fitted values suggested a pattern on the linear, but not on the logarithmic scale (Fig. 2). Therefore, hereafter we only considered models with ln(density) as the fixed covariate. Graphs of residuals versus ln(density) suggested a relationship between residual variance and variable ln(density), so possible heteroscedasticity was taken into account by supposing the residual variance to be proportional to $\ln(\text{density})^{2\delta}$, where δ is an unknown parameter. This heteroscedasticity was confirmed by the model selection since a heteroscedastic model comprising area and year within area random effects was selected among the six possible combinations (see Table 3). Random effects and standardised residuals were successfully checked for normality. Under this random structure, the SPCI appeared to be highly correlated to the variable ln(density) (conditional $F(1,9) = 56.7$, $P < 0.0001$).

The k^{th} observation of SPCI for area i and year j therefore is modelled as:

$$\text{SPCI}(i,j,k) = \mu + \alpha.\ln(\text{density}(i,j)) + b^{area}(i) + c^{year(area)}(j) + \varepsilon(i,j,k),$$

where μ and α represent fixed coefficients and b^{area} and

Table 3. Selection of the random part of the model having SPCI: $\mu + \alpha.\ln(\text{density})$ as the fixed part. The selected model, with the lowest AIC, is in italics. The selection of a model with a residual variance proportional to $\ln(\text{density})^{2\delta}$ indicates heteroscedasticity; df = degrees of freedom, or number of independent parameters in the model.

Random factors	Residual variance	df	AIC
Area+year	σ^2	5	147.1
Area	σ^2	4	145.3
None	σ^2	3	155.7
Area+year(area)	*$\sigma^2.\ln(\text{density})^{2\delta}$*	*6*	*123.3*
Area	$\sigma^2.\ln(\text{density})^{2\delta}$	5	134.8
None	$\sigma^2.\ln(\text{density})^{2\delta}$	4	149.2

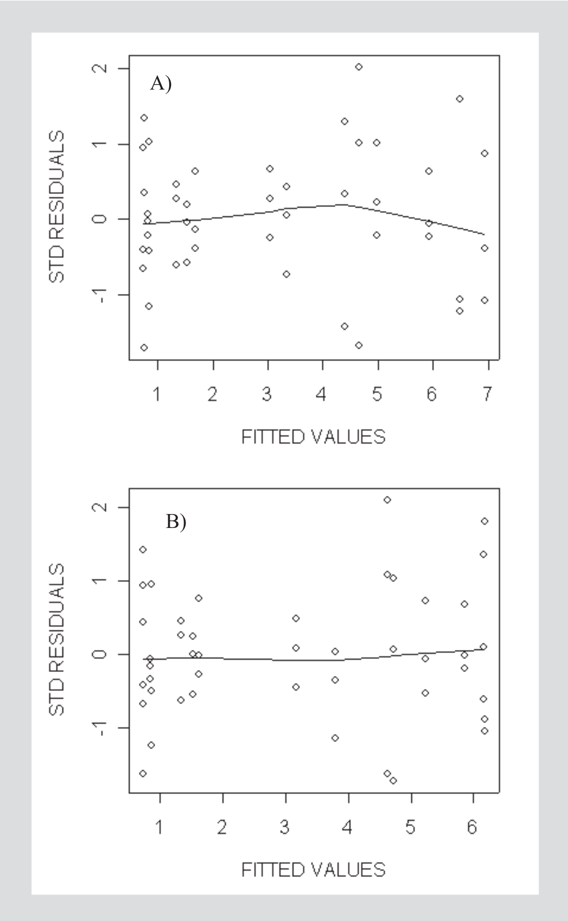

Figure 2. Distribution of residuals of the complete models with density (A) and ln(density) (B) as the fixed part. The model SPCI = f(ln(density)) was selected because the residuals of the model SPCI = f(density) show a pattern of dependence on the density.

$c^{year(area)}$ represent normal random independent variables with mean 0 and variances representing the inter-site and inter-year within site variances, respectively. The residuals $\varepsilon(i,j,k)$ are normal random variables independent of b^{area} and $c^{year(area)}$ and with heteroscedasticity accounted for as indicated earlier.

Detection of changes in rabbit density with the SPC

To evaluate the capacity of SPC measures to detect local changes in rabbit abundance over time, between 1994-1995 and 1995-1996, and with the help of a Mann-Whitney U-test, on each area we compared the trend in estimated density, which showed non-overlapping confidence intervals to the trend in the SPCI, which was determined to be significant (Table 4). In four cases out of 10, both density and SPCI were estimated to have changed significantly in the same direction. In two cases, none changed significantly. In two other cases, the density changed, but the SPCI did not. In the last two cases, the SPCI changed, but the density did not. In no case did the density significantly change in one direction and the SPCI in the opposite direction.

Table 4. Changes in the rabbit population in each area during the three sampled years (1994-1996) as measured by the CMR density estimate or by the SPC index. Significant increases (↗) or decreases (↘) are indicated; = indicates no significant difference, but a clear tendency when followed by an arrow in parentheses.

Area	Period	Density change	SPCI change
Chèvreloup	1994-1995	↘	↘
	1995-1996	↘	↘
Cerizay	1994-1995	↗	↗
	1995-1996	↗	=
Donzère	1994-1995	= (↘)	= (↘)
	1995-1996	= (↗)	= (↗)
La Chevallerais	1994-1995	↘	↘
	1995-1996	=	↗
Lalinde	1994-1995	=	↘
	1995-1996	↘	=

Discussion

The aim of our study was to test an abundance index against CMR, considered to be a reference method, in five different areas. The first point of discussion concerns the validity of the results given by the CMR. The goodness-of-fit tests demonstrated that the underlying assumptions of the Jolly-Seber models were generally met. Two basic assumptions were made in our work. The first one was that the average number of sightings of a rabbit during the three recapture sessions in a primary sampling period was identical for marked and unmarked animals. It is an underlying assumption of CMR models that capture and marking should not affect recapture probability. Generally, trap response (trap-happiness or trap-shyness) is a major source of unequal catchability. To minimise this, we used different techniques for capture and recapture, as recommended by Seber (1982). Therefore, the trap-dependence detected in La Chevallerais does not seem biologically sound and the significance of TEST 2 is probably due to the small sample size. The second assumption is that the probability of detecting a rabbit was the same for marked and unmarked animals, whereas marked rabbits obviously seem to be more detectable. However, resightings were made by walking through the study areas to stimulate movement of the animals. Therefore, we assumed that marked and unmarked rabbits had an equal probability of being resighted according to the immediate detectability of a moving animal. For these reasons, the density estimates were considered to be accurate. As expected, the estimated densities varied over a large range which is representative of most European populations of rabbits. Moreover, we recorded temporal variations in the estimated numbers of rabbits at several sites during the study. In Donzère, the decrease observed in 1995 was due to a severe outbreak of myxomatosis. The La Chevallerais area was managed by hunters, and most rabbits lived in artificial warrens. A lack of maintenance of these warrens was responsible for a decrease in habitat quality and therefore for the decline of the population. Conversely, the increase in Cerizay was due to efficient hunting management rules. A severe outbreak of rabbit viral haemorrhagic disease (RHD) was responsible for the major decrease in population size at the Chèvreloup arboretum in 1995. Mortality rates were estimated by an enumeration method which showed that up to 88% of the adults and 99% of the juveniles died during 1995 (Marchandeau et al. 1998, 2000). One may notice that, for this particular area, the decrease in population size, estimated by both SPC and CMR, agrees with the mortality rates recorded during the same period.

The non-linear relationship between SPCI and density shows that the index is not proportional to density. The underestimation given by SPC increases with density, showing a decrease in the sensitivity of the method to high densities. This density-dependent pattern was described as "the index may reach a 'saturation point', beyond which it is little influenced by additional increments in population size" (Conroy 1996). A similar saturation effect had already been noticed in rabbit spotlight counting (Fletcher et al. 1999). When density is low, the observer would be more attentive to detect the few rabbits present and, inversely, when density is high, not all the rabbits can be detected (Robinson & Wheeler 1983). Moreover, at high density, a group-size effect could be responsible for an increase in vigilance behaviour inducing a lower detectability of the rabbits (Roberts 1988, Lima 1995). Furthermore, in two cases the method suffers from a lack of sensitivity as it did not detect an actual change in population size. This may be due to a lack of power of the Mann-Whitney U-test with very small samples.

Most attempts to validate abundance indices are based on the correlation of the index with density, and/or on the precision of the index (Parer 1982, Wood 1988, Moller et al. 1996). According to these criteria, one could consider the SPC to be a reliable method to estimate rabbit population size. However, a more thorough study of the characteristics of this index shows that it is highly dependent on area and year. The significance of the area effect shows that the SPC is unsuitable to compare results obtained in different areas. This effect can be easily explained by variations in rabbit detectability as a function of landscape characteristics and observers (Thompson et al. 1998, Anderson 2001). Such results were already recorded for spotlight counts and prevent these abundance indices from being used for comparisons between areas (McCullough 1982, Ralls & Eberhardt 1997). The year effect is more problematic. It means that, in the same area, inter-annual changes in the index cannot be compared. This effect may also be related to variations in rabbit detectability (Thompson et al. 1998, Anderson 2001). Since the counts in each area were made by the same observer every year, one may assume that the observer effect probably did not affect the index value, but this effect could be important in surveys carried out by several observers. Among the environmental effects (Anderson 2001), meteorological conditions and also vegetation characteristics may have changed between years. The changes in vegetation characteristics could be related to changes in crop-rotations and/or to changes in vegetation height or density. One may observe that the two cases of index change in a stable population were recorded in the areas where the landscape changed between years, i.e. La Chevallerais and Aubas, due to changes in the crops. Finally, rabbit behaviour may also affect the detectability of the animals. For most species, the event of counting one animal only depends upon its presence inside the range of the spotlight and its sightability. For the rabbit, which spends part of its time in warrens, another condition is required since it has to be above ground at the time of the count. The proportion of rabbits that are above ground is highly variable and may be affected by environmental factors such as weather conditions and lunar phases (Rowley 1957, Mykytowycz & Rowley 1958). As our protocol aimed at comparing the index to an estimated density, we had to make the counts during a short period of time, i.e. for three consecutive nights or in the same week, to ensure that the number of live rabbits did not vary between repetitions of the counts. Therefore, in each area, these counts were often made under similar weather conditions and during similar lunar phases, reinforcing the possible effect of these factors. However, without this constraint imposed by our protocol, in the case of a survey for which such an index is used, this possible effect should be taken into account by a randomisation of the dates of these counts over a longer period.

In conclusion, one must keep in mind that the precision of the SPCIs is good and strongly correlated to actual density but is not a reliable method for monitoring population trends. This result confirms the necessity to validate the relationship between abundance indices and population density. Unless this validation is made, one must be careful when using abundance indices to monitor populations. Most attempts to study abundance indices are based on simple measures of precision that are necessary but not sufficient to assess the reliability of these indices. The underlying assumption of the use of an index is that changes in the index must be proportional in space and/or over time (Thompson et al. 1998). An area effect on the index leads to restriction of its use to a comparison of the temporal changes in population size in a defined area, but does not enable one to compare data collected in different areas. Such an index is reliable for monitoring most harvested populations for which inter-site comparisons are not of major interest. A year effect, as detected in our study, is more problematic since it does not enable one to use the index to monitor the changes over time in a given population. Other effects, such as observer effect or effects of lunar phases or weather conditions, may also affect the index. All these possible effects should be studied to standardise the conditions under which the indices should be applied to make sure that they will accurately reflect any changes in population size.

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