

# Monitoring low density populations: a perspective on what level of population decline we can truly detect

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## Abstract

*Monitoring low density populations: a perspective on what level of population decline we can truly detect.*— Monitoring of mammal species is an important part in detecting changes in their status. Efforts are based on a variety of direct and indirect methods and many low density populations are monitored through field signs. We present data on the endangered European red squirrel from Kidland Forest in the UK. We used cone transects to both record changes in seed availability and to monitor population trends. We examined the difficulty of accurately detecting population change when populations are low and field signs are patchily distributed. Current efforts would be sufficient to detect significant population declines of 50–75% in years with a modest squirrel population but not when they fall below one squirrel for every 20 ha of forest. The findings emphasise that monitoring aims have to be clearly defined with an awareness and understanding of what level of change the adopted methodological approach can reliably detect. We propose that mammal monitoring schemes need to be based on a pilot scheme to determine effect size and planned accordingly.

Key words: Squirrel, *Sciurus vulgaris*, Conservation, Power analysis.

## Resumen

*Seguimiento de poblaciones con baja densidad: una perspectiva de qué nivel de declive poblacional podemos detectar con certeza.*— El seguimiento de las especies de mamíferos es una parte importante de la detección de los cambios producidos en su estatus. Los esfuerzos van dirigidos hacia diversos métodos directos e indirectos, y muchas poblaciones que presentan una densidad baja se monitorizan mediante rastros o signos de campo. En este trabajo presentamos datos de una especie en peligro, la ardilla roja, del bosque de Kidland en el Reino Unido. Se realizaron transectos de detección de piñas o conos para registrar tanto los cambios en la disponibilidad de semillas como para monitorizar las tendencias de la población. Examinamos la dificultad que presenta detectar con precisión los cambios poblacionales, cuando las poblaciones son pequeñas y los restos alimentarios de presencia están distribuidos de forma desigual. Los esfuerzos normales deberían ser suficientes para detectar disminuciones poblacionales significativas del 50–75% en años con una población de ardillas modesta, pero no cuando la densidad está por debajo de una ardilla cada 20 ha de bosque. Nuestros hallazgos enfatizan que los esfuerzos de seguimiento deben estar claramente definidos, con el conocimiento y la comprensión de qué nivel de cambio puede realmente detectar de forma fiable el enfoque metodológico adoptado. Proponemos que los seguimientos de mamíferos deben estar basados en un esquema piloto, con el fin de determinar el efecto del tamaño, y ser planificados consecuentemente.

Palabras clave: Ardilla, *Sciurus vulgaris*, Conservación, Análisis de potencia.

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## Introduction

Monitoring and data on the distribution and abundance of mammal species are important to the understanding and detection of changes in the environment. They inform conservation activities, help assess the impacts of pollution, road traffic schemes or land use change and indicate the spread of introduced alien species (e.g. Battersby & Greenwood, 2004; Fitzgibbon, 1997; Hlavac, 2005; Harris & Yalden, 2004; Kataev, 2005; Macdonald et al., 1998; Philcox et al., 1999).

Data from surveys or monitoring generally encompasses two types of information on the status of a species: presence/absence data, and data on abundance (Macdonald et al., 1998). Distribution data either at regional or national scale in Britain are usually sightings recorded at 1 km<sup>2</sup> resolution (e.g. Lurz et al., 2005) and these are submitted by the general public or wildlife organisations to local record centres. Monitoring within some sites may be at a much finer scale and can provide an index of population trends over time. Monitoring implies that it is repeated in the same defined study area and that it should be carried out systematically (Macdonald et al., 1998).

A large number of survey or monitoring methods in mammals are based on field signs. These include systematic surveys for spraints and tracks of otters (*Lutra lutra*, Strachan & Jefferies, 1996), snow tracking for pine martens (*Martes martes*, Zalewski 1999), sett surveys for badgers (*Meles meles*, Clements et al., 1988), systematic surveys for latrines and feeding stations in water voles (*Arvicola terrestris*, Strachan et al., 2000) or pellet counts for deer (e.g. Hemami & Dolman, 2005). For squirrels, monitoring methods based on field signs include visual transects (Gurnell et al., 2001), tracks (Andr n & Lemnell, 1992), drey counts (Fitzgibbon, 1997; Wauters & Dhondt, 1988) and feeding remains (Gurnell et al., 2001, 2004). Additionally, hair-tube surveys (Gurnell et al., 2001) are used to also determine population size and abundance. Monitoring methods employed for squirrels focus on the detection of field signs or sightings rather than the area of habitat occupied. This is because home range size may increase when food is scarce and when densities are low, so area occupied is not a reliable measure of squirrel abundance. The various squirrel monitoring methods have been described in detail by Gurnell & Pepper (1994), and Gurnell et al. (2001, 2004).

Data based on squirrel field signs can be patchily distributed in space. They also vary with seasonal and annual patterns of food availability. This can lead to estimates with large associated errors making it difficult to calculate abundance accurately. In addition, it may result in insufficient statistical power to confidently determine whether a population change has truly occurred (Gurnell et al., 2004). Drey surveys are impractical in dense conifer forests and recent work (Gurnell et al., 2007) indicated that visual transects are very poor at

detecting red squirrels in Sitka spruce dominated forests. An additional limitation is that visual transects and hair-tube surveys are the only methods which can distinguish between the native red squirrel (*Sciurus vulgaris*) and the introduced grey squirrel (*S. carolinensis*) which has become naturalized in the UK and in regions of Continental Europe. However, hair-tube surveys are costly in terms of time and require expensive equipment and experienced staff (Gurnell et al., 2001).

In the UK, the most commonly used method to monitor squirrel presence and abundance in red squirrel-only areas are cone transects. Whilst this method cannot distinguish between squirrel surveys, it is deemed more reliable than visual transects, cheaper than hair-tube surveys, and can be employed in the dense spruce forests of northern England and Scotland where visual transects do not work (Gurnell et al., 2001).

Here we present data on a 6-year monitoring scheme from Kidland Forest, a designated red squirrel reserve. Kidland, together with the adjacent Uswayford Forest in the Cheviots, form the most isolated squirrel reserves in Northern England. Located in valley systems within the Cheviot hills, they are surrounded by open moorland incapable of supporting populations of squirrels. Due to this isolation and therefore lack of immigration and emigration opportunities, local red squirrel populations are potentially affected by timber harvesting and forest restocking operations. Conservation management therefore needs to maintain a minimum area of seed-bearing trees and avoid fragmentation of the forest through harvesting. We discuss (i) observed changes in seed food availability; (ii) describe monitoring efforts at Kidland Forest and (iii) examine the difficulty of accurately detecting population change when populations are low and field signs are patchily distributed.

## Material and methods

### Study area

Kidland Forest is part of Kielder Forest District and is located in the Cheviot hills in Northumberland, north-east England. The woodland is dominated by Sitka spruce (*Picea sitchensis*) with smaller plantations of Japanese larch (*Larix kaempferi*), Scots pine (*Pinus sylvestris*), lodgepole pine (*Pinus contorta*), Douglas Fir (*Pseudotsuga menziesii*), Norway spruce (*Picea abies*) and small areas of broadleaves.

### Survey methodology

Red squirrels at Kidland Forest were monitored using cone transect lines (Gurnell et al., 2001). The area between two rows of planted trees was cleared for up to 70 m and all cones (fallen cones as well as squirrel feeding remains) were counted on an annual basis in late autumn of each year.

The data were used to calculate an average number of cones consumed by squirrels per unit area (m<sup>2</sup>) for each conifer species and an estimated annual cone crop.

Using the area for each conifer species of seed-bearing age an estimated total of consumed seed energy was calculated (table 1). From this, the number of squirrels that could have been supported by the energy consumed can be derived by using an estimate of the annual squirrel energy requirement (Grönwall (1982): red squirrel energy requirement: 418.4 kJ/day ~ 152716 kJ/year; Gurnell (1987): 389.1 kJ/day ~ 142026 kJ/year). This estimate varies since the number and size of seeds within each cone is dependent on tree species, region and season. However, estimates derived in this way have been found to be significantly correlated with estimates from trapping data (Gurnell et al., 2004).

Using the methodology of Gurnell et al. (2004), an estimate of potential carrying capacity of a forest block can be calculated by multiplying minimum and average red squirrel densities with the area of mature (seed producing) tree species:

$$T_{\min} = \sum_{i=1}^n a_i \cdot d_{i,\min} \quad T_{\text{ave}} = \sum_{i=1}^n a_i \cdot d_{i,\text{ave}}$$

where  $T_{\min}$  and  $T_{\text{ave}}$  are the total population sizes for poor and average seed years,  $n$  is the total number of tree species stands of cone bearing age,  $a$  is the area of the tree species stands and  $d_{\min}$  and  $d_{\text{ave}}$  are the observed red squirrel density for that type of habitat in poor and average seed crop years.

To test for heterogeneity in the squirrel population we calculated the standardized Morisita index of dispersion (Myers, 1978) for each year, see

Table 1 Estimates of caloric values (kJ cone<sup>-1</sup>) for conifer species.

Tabla 1. Estimaciones de los valores calóricos (kJ cono<sup>-1</sup>) de las especies de coníferas.

Tree species	Energy (kJ/cone)	References
Scots pine	3.84	Wauters et al., 1992
Lodgepole pine	2.48	Smith, 1968
Norway spruce	9.6–17.2	Grönwall, 1982
Sitka spruce	5.3	Smith, 1981
Japanese larch	1.7	Grodzinski & Sawicka-Kapusta, 1970
Douglas fir	6.22	Smith, 1968
European Larch ( <i>Larix decidua</i> )	2.3	Grodzinski & Sawicka-Kapusta, 1970

Table 2. Estimates for squirrel densities in different crop types are based on fieldwork in Kielder Forest and similar habitats in the literature, and relate to the minimum number of adults (and post dispersal subadults recruited into the population) alive.

Tabla 2. Las estimaciones de las densidades de ardillas en función de la producción anual de semillas se basan en el trabajo de campo en el bosque de Kielder y en trabajos en hábitats similares que hallamos en la literatura, y se relacionan con el número mínimo de adultos vivos (y subadultos post-dispersión) reclutados en la población.

Tree species	Red squirrel density (ha <sup>-1</sup> )	Source
Sitka spruce	0.02–0.20	Lurz et al., 1998
Norway spruce	0.12–0.41	Lurz et al., 1998
Pine	0.16–0.43	Halliwell, 1997; Lurz et al., 1998
Larch	0.21	Garson & Lurz, 1998
Other conifers	0.03–0.80	Boby, 1978; Lurz, 1995

Table 3. This index is independent of both population density and sample size, and the value  $I_p$  ranges from  $-1.0$  to  $+1.0$ , with 95% confidence limits at  $-0.5$  and  $+0.5$ . Random patterns of dispersion give an  $I_p$  of zero, clumped patterns above zero, uniform patterns below zero.

#### Power analysis

Before calculations of statistical power can be made it is necessary to ensure that the number of transects taken does not constitute such a large proportion of the total number of possible transects that the precision of the calculated power will require correction. The finite population correction,  $fpc$  (Thompson, 2002) was calculated:

$$fpc = \sqrt{\frac{N - n}{N - 1}}$$

where  $n$  is the number of samples taken from the population of possible samples  $N$ . As  $n$  approaches  $N$ , the sampling variance approaches zero and the precision obtained from larger sample sizes becomes more significant. Conversely, if  $fpc$  is close to unity then no correction has to be made.

An *a priori* power analysis for the Wilcoxon–Mann–Whitney  $U$ -test is conducted by first performing an *a priori* power analysis for the  $t$ -test for means. If the  $t$ -test model is valid, and  $N_t$  designates the sample size necessary for the  $t$ -test to achieve some given power  $(1 - \beta)$ , then the sample size  $N_u = N_t / A.R.E.$  yields approximately the same power for the  $U$ -test. A.R.E. denotes the asymptotic relative efficiency (or Pitman efficiency) of the  $U$ -test relative to the  $t$ -test which is  $3/\pi = 0.955$  (see Lehmann, 1975).

The power of a paired  $t$ -test was calculated using the method of Kraemer & Thiemann (1987). It is first necessary to calculate the effect size of the observed decline, which is given by:

$$\Delta = \frac{\delta}{[\delta^2 + 1/pq]^{1/2}}$$

where  $p$  is the proportion of samples in year 1,  $q$  is the proportion of samples in year 2, and  $\delta$  is Glass's effect size. Glass's effect size is given by  $\delta = (\mu_1 - \mu_2) / \sigma$ , where  $\mu_1$  is the population size in year 1,  $\mu_2$  is the population size in year 2, and  $\sigma$  is the pooled standard deviation. The effect size  $\Delta$  for each pair of consecutive years (2001/2002, 2002/2003, etc.) was presented against the sample size (adjusted by the A.R.E. as discussed above).

We employed a two-year comparison because an intervening mast year between the two survey points would mask any decline which may be present. Alternatively, if the population declines in both subsequent years, the difference between year 1 and year 3 will naturally be greater than between year 1

and 2. One would therefore think that with a bigger effect size, more power could be obtained. However, since the variance is pooled between years it is larger in the former case, so a *greater* change is needed to confidently detect its presence. Estimates of power therefore get lower as the gap between sampling intervals increases. Finally, from a conservation perspective, when a population is potentially declining it may not be viable to wait several years before we can be confident that the decline is actually occurring.

We used the same methodology to calculate the power to detect a specific decline in squirrel population size, by replacing  $\mu_2$  in the above equations with a population size reduced artificially by a certain percentage (12.5%, 25%, ..., 87.5%).

To determine the ability to detect a change in a "healthy" population of squirrels, we calculated power based on the data for 2001 for  $\mu_1$ , and the pooled standard deviation between 2001 and 2002 for  $\sigma$ . A second analysis determined the ability to detect a change in size of a population which had already suffered a substantial decline, using the population size in 2005 as  $\mu_1$ , and the pooled standard deviation between 2005 and 2006 for  $\sigma$ . In both cases we were interested in the power of the test to detect a real population trend at a known number of samples.

These analyses were dependent (in the absence of real data) on the standard deviation remaining at the observed levels following a large decline in population size. To test the impact of this assumption on the predictions of the power analysis, we calculated the number of transects required to achieve an 80% power for a range of standard deviations, using the mean population size in 2005 for  $\mu_1$ .

## Results

Seed crops varied strongly between years at Kidland Forest and ranged from 0.00–2.03 cones  $m^{-2}$  in pine and larch and from 0.4–1.2 cones  $m^{-2}$  in Sitka spruce over the last 6 years (fig. 1). Red squirrel feeding remains and choice of conifer cones broadly followed seed crops. However, cone availability at Kidland between the different conifer plantations was significantly clumped (table 3) and varied markedly between locations and transect lines. As a result, estimates of red squirrel abundance calculated from the cone transect lines were associated with a large errors and data were overdispersed (fig. 1).

A comparison of the potential carrying capacity for Sitka spruce in 2006 (635 ha of mature forest) with an estimate of the red squirrel population based on cone transect data illustrates the factors a forester can influence and manage for and natural fluctuations in populations size. Observed densities of red squirrels in Sitka spruce plantations range from 0.02–0.2 squirrels  $ha^{-1}$  (table 2). Depending on seed food availability this

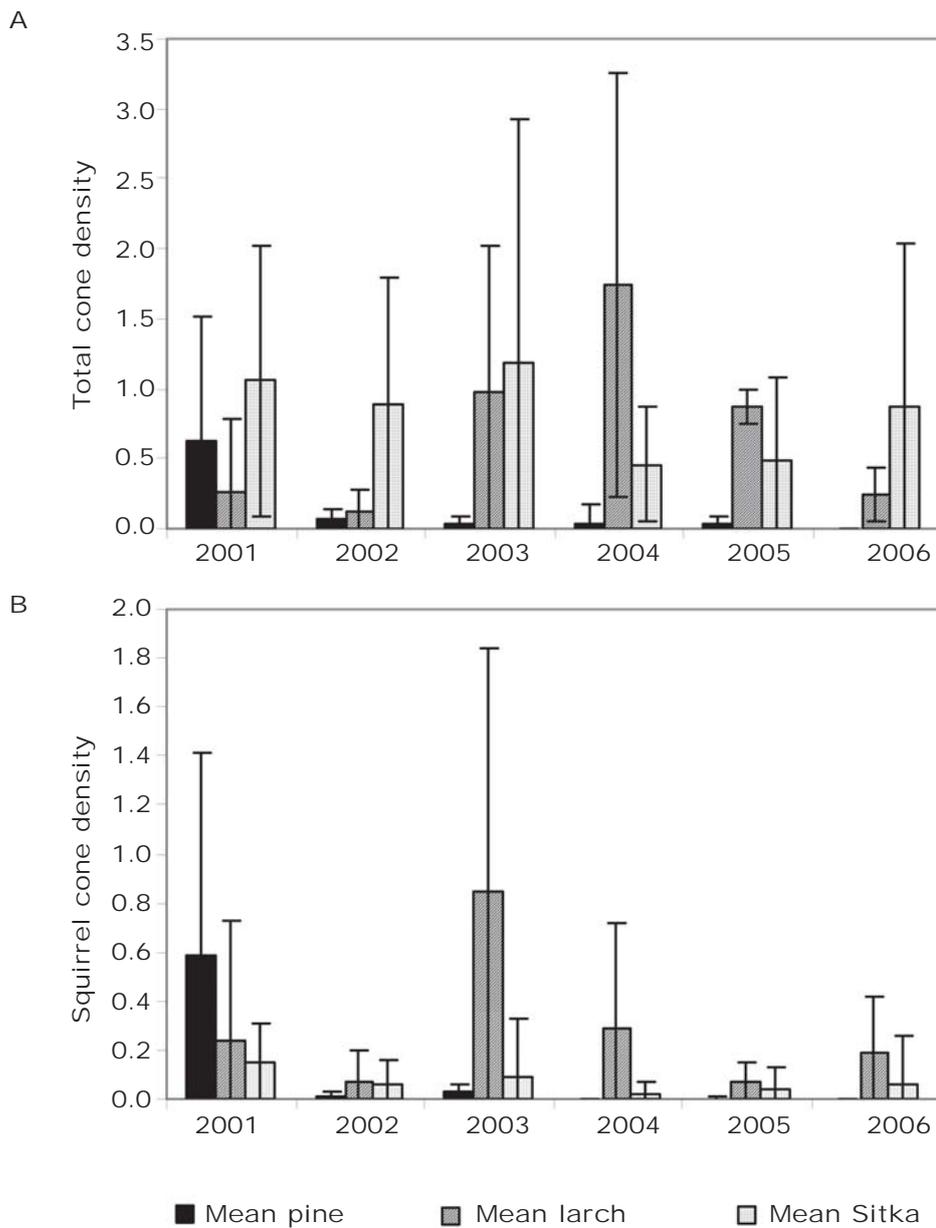


Fig. 1. Cone crop patterns for pine, larch and Sitka spruce at Kidland Forest: A. Total cone density (cones m<sup>-2</sup>) for each year; B. The amount of cones (m<sup>-2</sup>) stripped by squirrels.

*Fig. 1. Patrones de recolección de conos para los pinos, los alerces y la píceca de Sitka en el bosque de Kidland: A. Densidad total anual de conos (conos m<sup>-2</sup>); B. Cantidad de conos (m<sup>-2</sup>) descortezados por las ardillas.*

would result in a potential carrying capacity of the Sitka spruce plantations at Kidland Forest of 13–127 squirrels. The plantations of larch (34 ha) would approximately support 7 and the pine plantations (107 ha) 17–46.

Population size for red squirrels estimated from 2006 Sitka spruce cone transect data, the mean

density ( $\pm 1$  sd) of squirrel feeding signs ( $0.06 \pm 0.197$ ) and seed energy values (table 1) give an estimate for the average and upper limit of 13–57 squirrels for the Sitka spruce. In 2006 pine crops failed and the very poor cone crop in larch would at most have supported two squirrels. Whilst managers can influence the lower and upper

Table 3. Standardized Morisita index ( $I_p$ ) for squirrel feeding signs for each year. Values above 0.5 indicate significant clumping of the animal's distribution.

*Tabla 3. Índice de Morisita estandarizado para los rastros alimentarios de la ardilla, para cada año. Los valores superiores a 0,5 indican una agrupación significativa de la distribución de animales.*

Year	$I_p$
2001	0.57
2002	0.55
2003	0.57
2004	0.61
2005	0.54
2006	0.56

bounds of habitat carrying capacity, they have no control over fluctuations in seed crop size and thus annual squirrel abundance. The estimated population of red squirrels at Kidland for 2006 is currently near the lower third of the forest's potential carrying capacity.

For the calculation of the finite population correction it was first necessary to estimate the total number of potential transects available to be sampled. The total area of mature forest at Kidland is 799 ha. The average area of a cone transect was 40.9 m<sup>2</sup>, thus the total number of possible transects ( $N$ ) is therefore 195,522. The maximum combined number of transects used between two years ( $n$ ) was 63. This yields an  $fpc$  of 0.9998, which is negligible and therefore cannot affect the estimation of power.

Examining the 6 years of cone transect data for 2001–2006, figure 2 plots the effect size ( $\Delta$ ) calculated from 2001–2006 cone data against the number of samples needed to achieve a range of levels of statistical power. The calculated values for  $\Delta$  fail to achieve the suggested value for statistical power of 0.80 (Cohen, 1988) at the given sample sizes. This implies that a statistically significant trend in population size has insufficient replication to confidently detect a trend which is really there.

The results clearly show that current sample sizes of around 35 transects a year are not sufficient to detect small changes in effect and thus population size. This is especially true for years where the squirrel population is low (few feeding signs) and the field signs are patchily distributed across the forest. When concerned about the population decline of a rare species a more conservative approach would be to increase the likelihood

of declaring a decline has occurred, when in fact it has not—in effect increasing the rate of false positives (i.e. significance) with the benefit of simultaneously decreasing the rate of false negatives (i.e. power). Figure 2 therefore also demonstrates the impact of a 10% level of significance on the calculated number of samples required for each effect size  $\Delta$  and level of power. The highest level of power achieved was approximately 70% (for 2003–2004) rather than approximately 50% power assuming a 5% level of significance.

Consequently, the *a priori* analysis of the sample size required to achieve statistical power (fig. 3) is particularly useful in planning future monitoring programmes. The survey effort currently employed would be sufficient to detect significant population declines of 50%–75% in years with a modest red squirrel population of 0.05 squ/ha<sup>-1</sup> or greater as observed in 2001 (fig. 3A). However, when the population sizes are small ( $\leq 0.02$  squ/ha<sup>-1</sup>; fig. 3B) the statistical test does not achieve even a 50% power even following the maximum modelled population decline of 87.5%. The method would still indicate presence of squirrels based on the presence of feeding signs but any statistical comparisons between years lacks in sample size. Figure 4 illustrates that in pairs of years with large variations, such as from 2005 to 2006, an economically and logistically impractical number of sample transects (> 1,000) would be required to achieve adequate levels of power.

## Discussion

The findings of our study highlight the difficulties of monitoring small populations of endangered mammals in habitats where surveys based on field signs are the only option. Kidland Forest is a rare case where conservation management (Lurz et al., 2003) has been followed by annual monitoring with the clear aim to assess the impact of forest operations on the viability of a red squirrel population. It provides a medium-term data set with which to statistically investigate the limits of field sign surveys to reliably detect population change.

Cone crops at Kidland varied strongly temporally and spatially between 2001–2006. The patchiness and annual variability of field signs across the forest and the resulting large error estimates make it difficult to calculate squirrel abundance accurately. This may mask real population change and may make it difficult to distinguish the relative impacts of natural fluctuations in seed crops (Gurnell, 1983, 1987) and squirrel declines as a result of forest operations or other factors.

The examination of 6 years of field data clearly shows that the current sampling programme is not sufficient to detect small changes in population size. Current efforts would be sufficient to detect significant population declines of 50–75% in years with a modest red squirrel population but not when

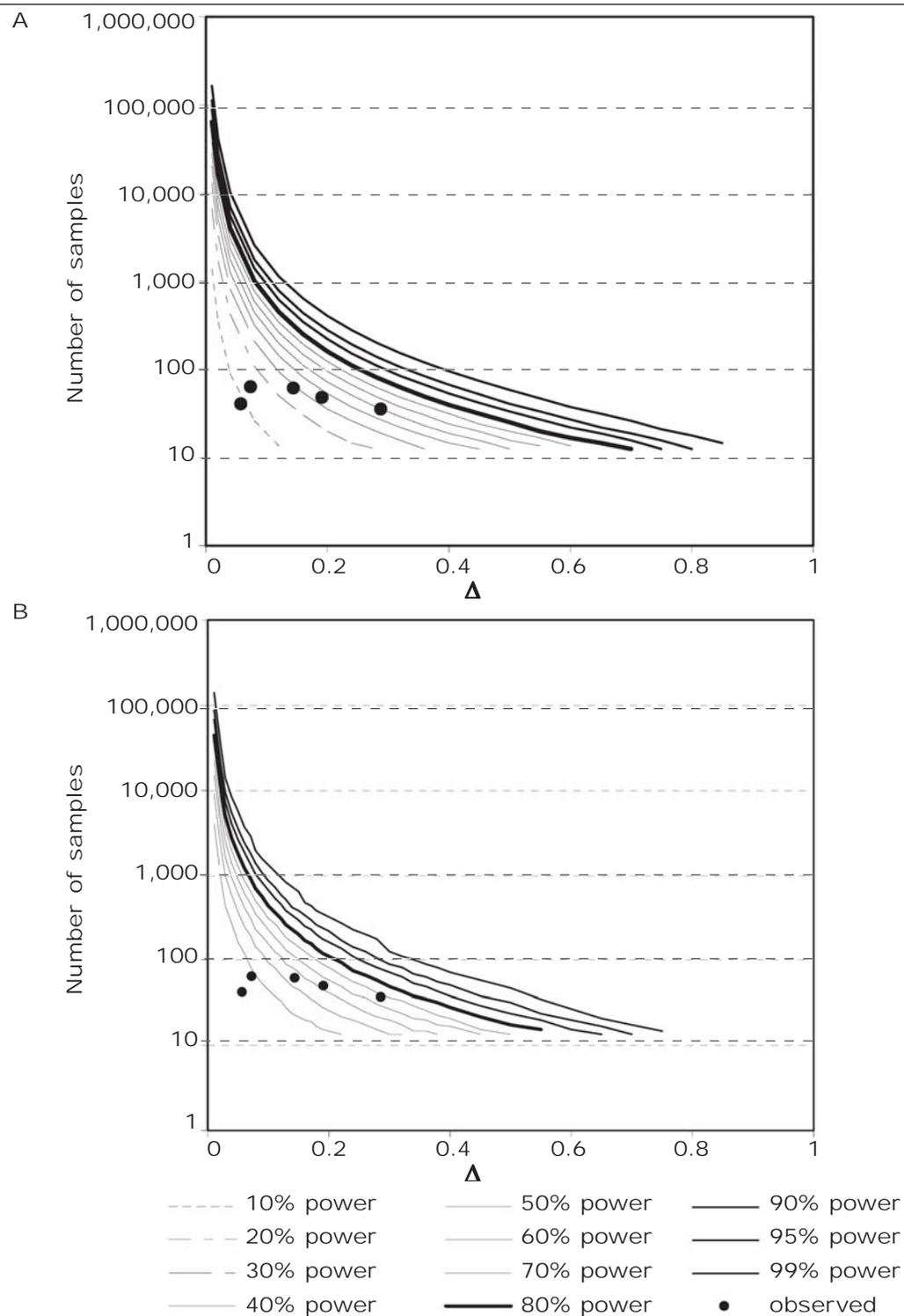


Fig. 2. Graph illustrating the tabulated values for power at each value of  $\Delta$  and sample size for a one-sample  $t$ -test at the 5% (A) and 10% (B) levels of significance, using the method of Kraemer & Thiemann (1987). Observed values from cone transects at Kidland Forest are indicated by circles.

Fig. 2. Gráfico que ilustra los valores tabulados de la potencia para cada valor de  $\Delta$  y cada tamaño de la muestra para un test- $t$  de una sola muestra, a los niveles de significación del 5% (A) y el 10% (B), utilizando el método de Kraemer & Thiemann (1987). Los valores observados a partir de los transectos de conos del bosque de Kidland se hallan destacados mediante círculos.

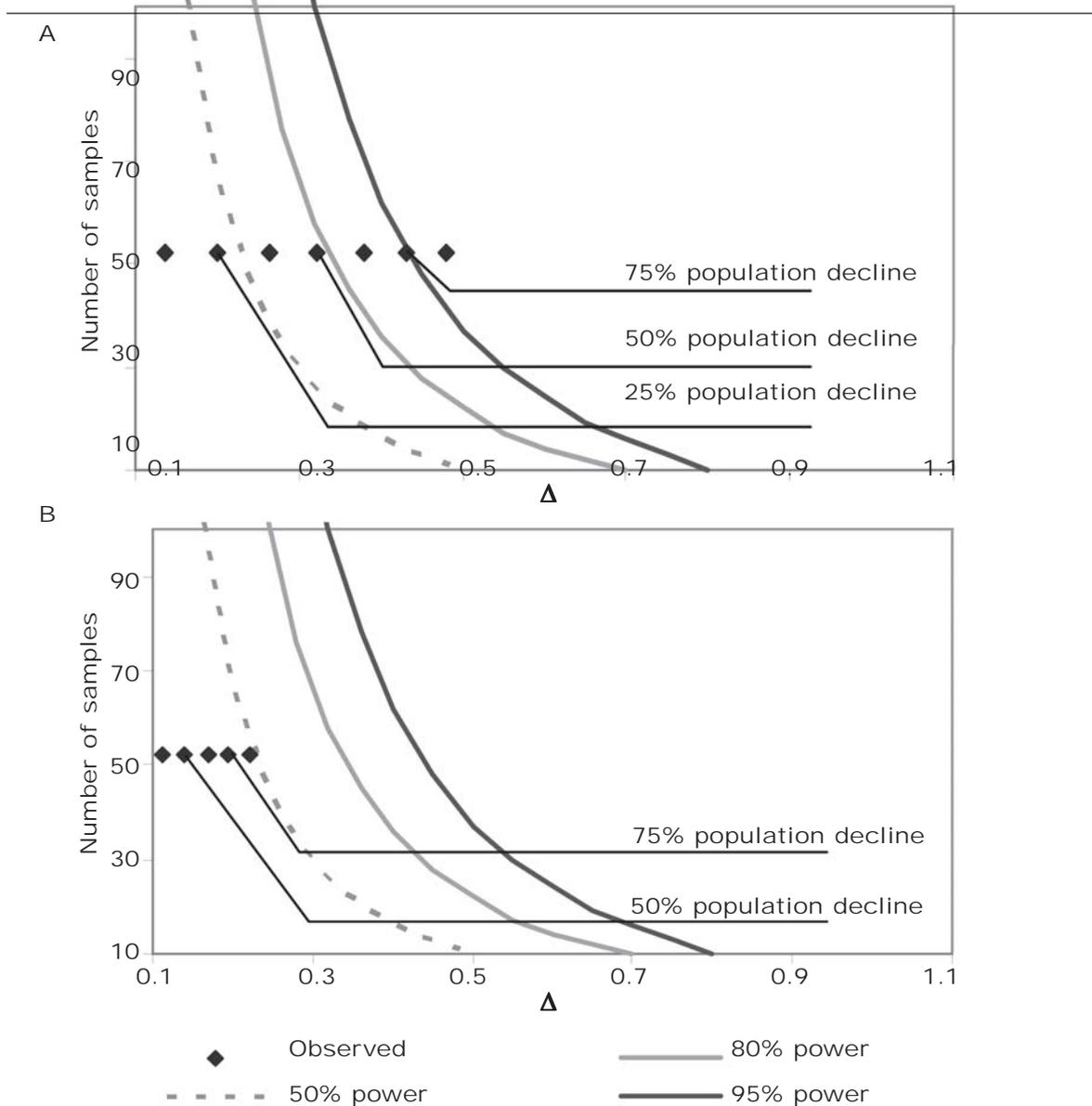


Fig. 3. An *a priori* power analysis of the sample size required to achieve statistical power: A. Analysis using highest observed population (2001–2002) to calculate effect size  $\Delta$ ; B. Analysis using lowest observed population (2005–2006) to calculate effect size  $\Delta$ .

*Fig. 3. Un análisis de potencia a priori del tamaño de la muestra requerido para alcanzar un poder estadístico: A. Análisis utilizando la población observada de mayor tamaño (2001–2002) para calcular la fuerza del efecto  $\Delta$ ; B. Análisis utilizando la población observada de menor tamaño (2005–2006) para calcular la fuerza del efecto  $\Delta$ .*

squirrel populations fall below 1 squirrel for every 20 ha of forest. Using field signs when densities are this low would still detect the presence of red squirrels but any meaningful statistical comparisons would require sample sizes of > 1,000 transects, a survey effort which is out of proportion in terms of time and cost for the data obtained. We also demonstrate the effects of increasing the critical level of significance

on statistical power, on the understanding that it is better to assume a population decline where there was none than to fail to detect a decline where there was one. However, in this study increasing significance to 10% still failed to achieve a statistical power of 80%.

The study findings underline the importance of applying an integrated monitoring approach in which

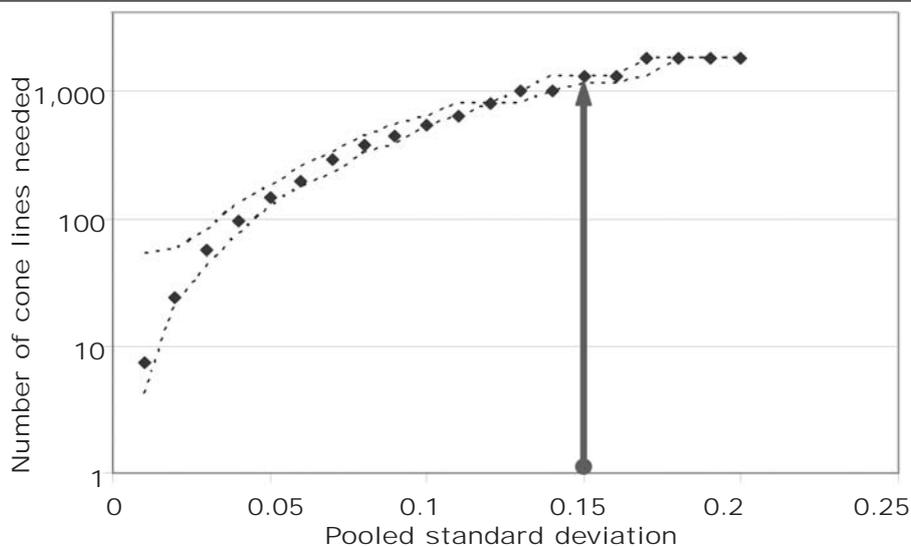


Fig. 4. The number of cone lines (pooled over two years) needed to achieve 80% confidence of detecting a real change in population size (one-tailed Mann–Whitney  $U$ -test, 5% significance). The dotted lines represent the number of cone lines needed when the upper and lower 95% confidence intervals for the pooled standard deviation are used in the calculation. The arrow indicates the observed pooled standard deviation.

Fig. 4. Número de líneas de conos (reunidos durante dos años) necesarias para alcanzar un 80% de confianza al detectar un cambio real en el tamaño de la población (test  $U$  de Mann–Whitney de una cola, 5% de significación). Las líneas de puntos representan el número de líneas de conos necesarias cuando se utilizan para el cálculo los intervalos de confianza del 95% superior e inferior para la desviación estándar reunida. La flecha indica la desviación estándar reunida observada.

more than one method is combined (Flowerdew et al., 2004). Monitoring at Kidland without an independent assessment of carrying capacity would not be able to distinguish the relative population declines from changes in seed availability and potential impacts from harvesting operations, disease outbreaks (Sainsbury et al., 2000; McInnes et al., 2006) or other factors.

The results also emphasise that monitoring aims have to be clearly defined with an awareness and understanding of what the adopted methodological approach can reliably detect. This is particularly true when monitoring small endangered populations based on widely distributed field signs. Very often the objectives of monitoring programmes are poorly defined (Yoccoz et al., 2001), and there is a need to consider carefully: (i) the types of data to be collected, (ii) the precision with which population change can be detected for an appropriate sampling method and effort and (iii) the cost effectiveness of methods given budgetary constraints (Manley et al., 2004; Gaidet–Drapiet et al., 2006).

We therefore propose that the setting up of mammal monitoring schemes is based on a pilot study that allows the estimation of effect size. From this, statistical power analysis can inform the moni-

toring scheme with respect to adequate sample size and/or the magnitude of population change the proposed scheme can confidently detect.

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#### References

- Andrén, H. & Lemnell, P., 1992. Population fluctuations and habitat selection in the Eurasian red squirrel *Sciurus vulgaris*. *Ecography*, 15: 303–307.
- Battersby, J. E. & Greenwood, J. J. D., 2004. Monitoring terrestrial mammals in the UK: past, present and future, using lessons from the bird world. *Mammal Review*, 34(1–2): 3–29.

- Boby, G. Y., 1978. A contribution to the ecology of the Altaian squirrel (*Sciurus vulgaris altaicus*) acclimatised in the Teberdinsky State Reservation. *Zoologicheskii Zhurnal*, 57: 253–259.
- Cohen, J., 1988. *Statistical Power Analysis for the Behavioral Sciences*, 2nd edn. Lawrence Erlbaum Associates, Hillsdale, New Jersey.
- Fitzgibbon, C. D., 1997. Small mammals in farm woodlands: The effects of habitat, isolation and surrounding land-use patterns. *Journal of Applied Ecology*, 34(2): 530–539.
- Flowerdew, J. R., Shore, R. F., Poulton, S. M. C. & Sparks, T. H., 2004. Live trapping to monitor small mammals in Britain. *Mammal Review*, 34(1–2): 31–50.
- Gaidet–Drapier, N., Fritz, H., Bourgarel, M., Renaud, P. C., Poilecot, P., Chardonnet, P., Coid, C., Poulet, D. & Le Bel, S., 2006. Cost and efficiency of large mammal census techniques: comparison of methods for a participatory approach in a communal area, Zimbabwe. *Biodiversity and Conservation*, 15(2): 735–754.
- Garson, P. J. & Lurz, P. W. W., 1998. Red squirrel monitoring: the potential of hair–tubes for estimating squirrel abundance in conifer plantations dominated by Sitka spruce: *Report to JNCC, Contract, 76–01–68*.
- Grodzinski, W. & Sawicka–Kapusta, K., 1970. Energy values of tree–seeds eaten by small mammals. *Oikos*, 21: 52–58.
- Grönwall, O., 1982. Aspects of the food ecology of the red squirrel (*Sciurus vulgaris* L.). Ph. D. Thesis, University of Stockholm.
- Gurnell, J., 1983. Squirrel numbers and the abundance of the seeds. *Mammal Review*, 13: 133–148.
- 1987. *The Red Squirrel*. Christopher Helm, London.
- Gurnell, J., Lurz, P. W. W., McDonald, R., Cartmel, S., Rushton, S. P., Tosh, D., Sweeney, O. & Shirley, M., 2007. Developing a monitoring strategy for red squirrels (*Sciurus vulgaris*) across the UK Report to JNCC and PTES, London, UK.
- Gurnell, J., Lurz, P. W. W. & Pepper, H., 2001. *Practical Techniques for surveying and monitoring squirrels*. Forestry Commission Practice Note 11, Forestry Commission, Edinburgh.
- Gurnell, J., Lurz, P. W. W., Shirley, M. D. F., Cartmel, S., Garson, P. J., Magris, L. & Steele, J., 2004. Monitoring red squirrels *Sciurus vulgaris* and grey squirrels *Sciurus carolinensis* in Britain. *Mammal Review*, 34: 51–74.
- Gurnell, J. & Pepper, H., 1994. *Red squirrel conservation: field study methods*. Research Information Note No. 255, Forestry Commission, Farnham.
- Halliwell, E. C., 1997. Red squirrel predation by pine martens in Scotland. In: *The conservation of red squirrels, Sciurus vulgaris* L.: 39–48 (J. Gurnell & P. W. W. Lurz, Eds.). London: Peoples Trust for Endangered Species.
- Harris, S. & Yalden, D. W., 2004. An integrated monitoring programme for terrestrial mammals in Britain. *Mammal Review*, 34(1–2): 157–167.
- Hemami, M. R. & Dolman, P. M., 2005. The disappearance of muntjac (*Muntiacus reevesi*) and roe deer (*Capreolus capreolus*) pellet groups in a pine forest of lowland England. *European Journal of Wildlife Research*, 51(1): 19–24.
- Hlavac, V., 2005. Increasing permeability of the Czech road network for large mammals. *Gaia–Ecological Perspectives for Science and Society*, 14(2): 175–177.
- Kataev, G. D., 2005. The state of the mammal community of boreal forest ecosystems in the vicinity of a nickel–smelting plant. *Russian Journal of Ecology*, 36(6): 421–426.
- Kraemer, H. C. & Thiemann, S., 1987. *How Many Subjects?: Statistical Power Analysis in Research* SAGE Publications, Newbury Park.
- Lehman, E. L., 1975. *Nonparametrics: Statistical Methods Based on Ranks* Holden–Day, San Francisco, USA.
- Lurz, P. W. W., 1995. The ecology and conservation of the red squirrel (*Sciurus vulgaris* L.) in upland conifer plantations. Ph. D. Thesis, University of Newcastle.
- Lurz, P. W. W., Garson, P. J. & Ogilvie, J. F., 1998. Conifer species mixtures, cone crops and red squirrel conservation. *Forestry*, 71: 67–71.
- Lurz, P. W. W., Geddes, N., Lloyd, A. J., Shirley, M. D. F., Rushton, S. P. & Burlton, B., 2003. Planning a red squirrel conservation area: using a spatially explicit population dynamics model to predict the impact of felling and forest design plans. *Forestry*, 76: 95–108.
- Lurz, P. W. W., Hewitt, S. M., Shirley, M. D. F. & Bruce, J., 2005. Mammals in Cumbria: examples of what publicly collected records can tell us about the distribution and ecology of local species. *Carlisle Naturalist*, 13: 1–15.
- Macdonald, D. W., Mace, G. & Rushton, S., 1998. *Proposals for future monitoring of British mammals*. Department of the Environment, Transport and the Regions, London.
- Manley, P. N., Zielinski, W. J., Schlesinger, M. D. & Mori, S. R., 2004. Evaluation of a multiple-species approach to monitoring species at the ecoregional scale. *Ecological Applications*, 14(1): 296–310.
- McInnes, C. J., Wood, A. R., Thomas, K., Sainsbury, A. W., Gurnell, J., Dein, J. & Nettleton, P. F., 2006. Genomic characterization of a novel poxvirus contributing to the decline of the red squirrel (*Sciurus vulgaris*) in the UK. *Journal of General Virology*, 87: 2115–2125.
- Myers, J. H. 1978. Selecting a measure of dispersion. *Environmental Entomology*, 7: 619–621.
- Philcox, C. K., Grogan, A. L. & Macdonald, D. W., 1999. Patterns of otter *Lutra lutra* road mortality in Britain. *Journal of Applied Ecology*, 36(5): 748–762.
- Sainsbury, A. W., Nettleton, P., Gilray, J. & Gurnell, J., 2000. Grey squirrels have high seroprevalence to a parapoxvirus associated with deaths in red squirrels. *Animal Conservation*, 3: 229–233.

- Smith, C. C., 1968. The adaptive nature of social organization in the Genus of three squirrels *Tamiasciurus*. *Ecological Monographs*, 38: 31–63.
- 1981. The indivisible niche of *Tamiasciurus*: an example of non-partitioning of resources. *Ecological Monographs*, 51: 343–363.
- Thompson, S. K., 2002. *Sampling*. Second Edition. Wiley, New York.
- Wauters, L. A. & Dhondt, A. A., 1988. The use of red squirrel (*Sciurus vulgaris*) dreys to estimate population density. *Journal of Zoology, London*, 214: 179–187.
- Wauters, L., Swinnen, C. & Dhondt, A. A., 1992. Activity budget and foraging behaviour of red squirrels (*Sciurus vulgaris*) in coniferous and deciduous habitats. *Journal of Zoology*, 227: 71–86.
- Yoccoz, N. G., Nichols, J. D. & Boulinier, T., 2001. Monitoring of biological diversity in space and time. *Trends in Ecology and Evolution*, 16: 446–453.
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