Testing the reliability of pellet counts as an estimator of small rodent relative abundance in mature boreal forest

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Small rodents form an important group of prey for a number of predators in Canadian boreal forests, and monitoring their abundances annually is of prime interest for several research goals. We analyzed whether fecal pellet counts — used as an index of small rodent abundance (mainly voles) — are an accurate, rapid and inexpensive method for population monitoring in the boreal black spruce forest. Snap-trapping was used as a proxy to assess the relative abundance of small rodents, while counts of fecal pellet groups were conducted on circular plots superimposed to snap trapping grids. Captured rodents were mainly the southern red-backed vole (*Myodes gapperi*). Surveys were conducted during the high (2003) and declining (2004; intermediate level) phases of its abundance cycle. Surveys were carried out in mature forest only. Using generalized linear model (with Poisson error) for count data, we found a significant relationship between the abundance of fecal pellet groups and rodents captures per 100 trap-nights in 2003 and in 2004. However, in both cases, relationships were weak (pseudo-R^2 < 0.1). We hypothesize that such a lack of reliability in explaining variance in small rodent abundance is due to: (1) the high variability in rodent abundance, especially within season but also within and between years; and (2) the heterogeneous distribution patterns of fecal pellet groups. Our results thus suggest that fecal pellet count alone is a highly variable and inaccurate index of small rodent captures per 100 trap-nights (and ultimately of abundance) in the boreal black spruce forest on an annual basis.

Introduction

Measuring population abundances is a critical issue in ecology. Numerous research projects or wildlife management plans depend on accurate estimation of species abundance. There is a strong demand for reliable indirect estimators (Slade & Blair 2000) as capturing all individuals from a population is most of the time impossible (Hopkins & Kennedy 2004) and methods based on capture are generally logistically laborious, time-consuming and expensive (Hansson 1979, Lancia *et al*. 1994, Gibbs 2000). Indirect indicators can simply be defined as 'any measurable correlatives of density' (Caughley 1977) and are assumed to be related to actual or recent past abundance in some manner (Gibbs 2000). Barnes (2001) considers that the relationship

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occurring between an estimator and absolute abundance should exhibit low variance in order to be reliable.

For such considerations, various indirect estimators of abundance have been developed (Gibbs 2000) and some have been tested with or without success (Walker *et al*. 2000). Consequently, a wide diversity of relative abundance indices are commonly used in the field, such as hunting and fishing harvest estimators for game species (Krebs 1999), antler counts (Lancia *et al*. 1994) and aerial surveys (Potvin *et al*. 1992) for ungulates, spotlighting for the squirrel glider (*Petaurus norfolcensis*) (Goldingay & Sharpe 2004), winter track and carcass counts for mammals (Gibbs 2000) and fecal pellet counts (Krebs *et al*. 1987). The pellet count technique is now widely used by wildlife managers to estimate the abundance or habitat use of species such as snowshoe hare (*Lepus americanus*) (Krebs *et al*. 1987, 2001), mountain hare (*L. timidus*) (Angerbjörn 1983), brown hare (*L. europaeus*) (Langbein *et al*. 1999), mountain vizcachas (*Lagidium viscacia*) (Walker *et al*. 2000), wall lizard (*Podarcis muralis*) (Avery & Perkins 1989), spruce grouse (*Falcipennis canadensis*) (Huggard 2003), greater rhea (*Rhea americana*) (Herrera *et al*. 2004), deer (*Odocoileus* spp.) (Roseberry & Woolf 1991), elk (*Cervus elaphas roosevelti*) (Lehmkuhl *et al*. 1994), and elephants (*Loxodonta* spp.) (Barnes 2001). These often low cost indirect abundance estimators can be applied at large scale for relatively small logistics and time investments, especially for species found at low densities or that are difficult to capture and observe.

Small rodent populations from the boreal forest have been studied and monitored for several decades in the northern hemisphere, especially for their key role in the trophic chain as prey for numerous avian and terrestrial predators (Korpimäki 1981, Hanski *et al*. 1991, 2001). Consequently, fluctuations in small rodent abundance have a major effect on upper trophic levels (Hanski *et al*. 1991, 2001). However, estimating rodent abundances can be a logistically heavy task in boreal forests, and punctual estimations require several repeated samplings as small rodents exhibit cyclic fluctuations in abundance with a periodicity of 3 to 5 years (Hansson &

Henttonen 1988, Stenseth 1999, Cheveau *et al*. 2004). In boreal forest of eastern Canada, the cycle period was estimated to be 4 years (using large-scale datasets gathered at latitudes varying from 49° to 55°) (Cheveau *et al*. 2004, Côté *et al*. 2007). Trapping thus appears to be a time consuming way of assessing rodent abundances (Petty 1999). Actually, estimation of small rodent abundance is done directly by capture-recapture (Etcheverry *et al*. 2004) and trapping (Day *et al*. 1980, Côté *et al*. 2003), or indirectly by measuring the breeding success of avian predators (Sundell *et al*. 2004) and winter irruption of owls in southern latitudes of boreal forest (Cheveau *et al*. 2004, Côté *et al*. 2007). All of these indices show different precision levels.

In Fennoscandia, correlative evidence of the relationship between fecal pellet counts and abundance was previously explored by Hansson (1979) for field vole (*Microtus agrestis*) and bank vole (*Myodes glareolus*), but correlations of variable strength (i.e., linear regression and nonlinear power curve fit ranging from $r = 0.39$ to 0.86) were observed strictly for the first species in abandoned fields; no strong correlation was recorded for the second species in forest. In France, a method was successfully developed by Delattre *et al*. (1990) to estimate common vole (*M. arvalis*) abundance in grasslands based on numbers of burrow entrances, runways and droppings. Such a vole sign index (VSI) was also built by Petty (1999) using the presence/absence of runways, droppings and clippings (as forage index) to estimate field vole abundance in recently planted spruce forest in England. However, no clear evidence of the relationship between droppings and abundance has yet been assessed for small rodent species in mature boreal forests of North America.

The aim of the present study is thus to investigate the possible relationship between abundance of fecal pellets and of small rodents in the eastern Canadian boreal forest. To do so, we counted pellets and assessed rodent abundance using snap trapping, for all species pooled, during the spring and summer of 2003 and 2004 in mature black spruce forest. We found a significant relationship between rodent relative abundance and pellet counts in 2003 and 2004, but failed to explain a large part of the variability
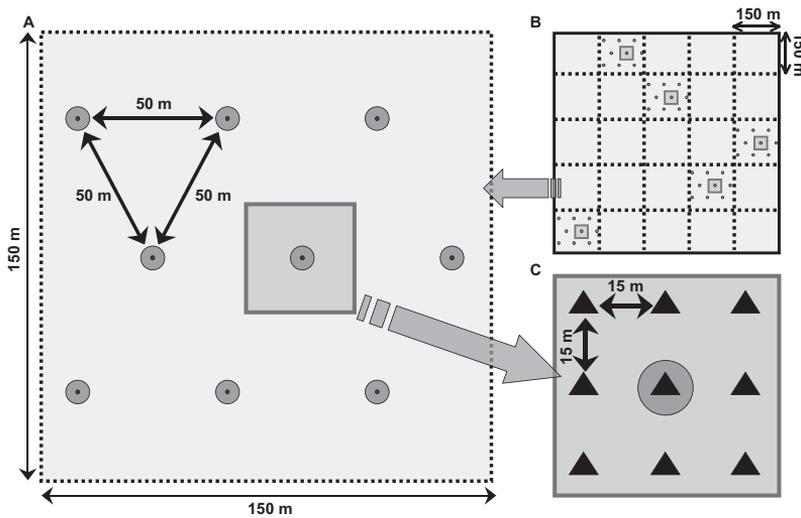
Fig. 1. Study setup. — **A**: A study grid consisting of 9 × 1-m radius sample plots (filled grey circles), arranged in three offset rows, 50-m apart for fecal pellet counts. — **B**: Five of these grids were set randomly in each site. — **C**: Nine snap-traps (black triangles) for rodent capture were placed 15-m apart in a 3 × 3 grid, centered on the centre plot of each of the five large grids.

in rodent relative abundance based exclusively on the abundance of pellet groups. We concluded that fecal pellet count alone is a highly variable and inaccurate index of small rodent captures per 100 trap-nights, at least in cyclic populations.

Materials and methods

Study area

This study was conducted in mature black spruce (*Picea mariana*) boreal forest, north of Lac St. Jean, Québec, Canada (50°09´N, 72°20´W). Mean elevation of the study area is 505 m. At the time of data collection, approximately 30% of the study area had been logged. Mature forest stands were mainly composed of black spruce, balsam fir (*Abies balsamea*), white birch (*Betula papyrifera*), jack pine (*Pinus banksiana*) and trembling aspen (*Populus tremuloides*) in order of decreasing abundance. Alders (*Alnus* spp.), American mountain ash (*Sorbus americana*), juneberry (*Amelanchier* spp.) and willows (*Salix* spp.) dominated the shrub stratum, and the most common ericaceous species in the understory were sheep laurel (*Kalmia angustifolia* L.), swamp laurel (*K. polyfolia*), Labrador tea *(Ledum groenlandicum* Oeder), leatherleaf (*Chamaedaphne calyculata*), cloudberry (*Rubus chamaemorus*) and blueberries (*Vaccinium myrtilloides*, *V. angustifolium*). Taxonomic nomenclature follows Farrar (1996).

Study design

We set up 20 study sites within logged landscapes in undisturbed and residual mature forest. Sites ranged above 85 ha in size (up to 1000 ha), were all composed of unharvested mature forest [mean age = 110.8 ± 30.9 years (SE)] and exhibited relatively similar stand structures but high inter-site variability (*see* St-Laurent *et al*. 2007). Study sites were randomly chosen from the available sites, and spaced by at least 1 km (mean distance between sites of 3.5 km) to limit pseudoreplication. In each of the 20 sites, we randomly placed five grids containing nine circular plots (1-m radius), systematically spaced 50 m apart in three offset rows (*see* Fig. 1), for a total sampling effort of 900 plots in 100 grids.

Fecal pellet surveys

Fecal pellet surveys were conducted during the spring of 2003 and 2004 in each of the 900 plots. Counts were done shortly after snow melt, before the onset of green-up, and all pellets were removed from each plot after counting. The plots were previously cleared in 2002, so counts refer to a single year in which pellets could be deposited. Groups of pellets were counted as done for surveys of snowshoe hare pellets (Krebs *et al*. 1987, 2001, St-Laurent *et al*. 2007). We considered one or several fecal pellets as a group of fecal pellets after having

observed that heaps were rarely composed of more than 10 droppings. This approach was used to limit bias caused by the possibility of missing a single pellet hidden in the moss substrate, and because rodent pellets are usually deposited in a clumped pattern (Pugh *et al*. 2003). We used 1 m radius circular plots rather than rectangular plots or small circular plots (0.155 m²) to increase the likelihood of recording fecal pellets and to reduce sample variance (Murray *et al*. 2002).

Snap trapping of small rodents

We assessed the relative abundance of small rodents in the 20 sites using snap-trapping, an efficient proxy of abundance for rodents when true abundance is not known (Day *et al*. 1980, Ecke *et al*. 2002, Côté *et al*. 2003). Moreover, snap-trapping allowed us to carry out precise species identification using bony palate characteristics for all captured rodents [*see* Lupien's (2002) identification key of morphological characteristics for small rodents of Québec]. In the centre of each of the 100 grids (five per site), we superimposed a small grid of nine (3 × 3) snap traps (traditional Victor™ trap, model 150, 4 × 1.75 inches) equally spaced by 15 m (Fig. 1) to ensure that fecal pellet counts were not directly related to the number of individuals captured by snap trapping. Snap traps were baited with peanut butter (Day *et al*. 1980) and set for two 24-hour capture periods. Trapping grids were visited during two consecutive days following setting; snap traps were re-baited or replaced when necessary. As snow cover remained until the beginning of June each year in the study area, small rodent surveys were conducted between mid-June and mid-July of 2003 and 2004. Capture effort was consequently of 90 trap-nights per site per year, and surveys were conducted in summer 2003 and spring 2004, for a total effort of 3600 trap-nights. Rodent capture was carried out approximately one month following pellet counts in 2003 and 2004. The relative abundance of small rodents was calculated using a trap-effort index to establish the number of captures per 100 trap-nights. Traps that were sprung but empty after 24 hours were considered as having a half interval of trapping (Nelson & Clark 1973).

The closest distance between two trapping grids was 150 m when two large sampling grids were randomly adjacent, which was not systematic. As Bowman *et al*. (2000) observed positive spatial autocorrelation for small rodents between 133 and 533 m, we could question the importance of such autocorrelation on rodent distribution within our sampling design. Nevertheless, we demonstrated in a companion study conducted with the same database that spatial autocorrelation accounts for less than 10% in explaining fluctuations in relative abundance at the grid scale (St-Laurent *et al*. 2007). Consequently, two adjacent trapping grids were considered to be statistically independent and our analyses were based on a sample size of 100 grids per year (20 sites × 5 grids per site; Fig. 1).

Data analyses

For each year, the abundance of fecal pellet groups was compared to the relative abundance of rodents, previously determined by snap trapping, at the grid scale (*n* = 100). As counts followed a Poisson distribution, we preferred to use a generalized linear model (GLM) with a Poisson error term and a log link function (i.e. log-linear model) (Quinn & Keough 2002) rather than simply transform the response variable with a power transformation. These GLMs were carried out separately for 2003 and 2004 datasets, using the GENMOD procedure in the SAS statistical package. Homoscedasticity was confirmed graphically and by GLM procedure. Following Krebs *et al*. (1987), we explored the relationship between the mean abundance of fecal pellet counts and variance in those counts, following Taylor's power law (Taylor 1961), using a standard linear regression (GLM procedure). All statistical analyses were carried out using SAS 9.1 statistical package (SAS Institute 2004, Cary, North Carolina, USA).

Results

We captured 409 small rodents in 2003 (i.e. upper phase of the rodent abundance cycle), and 192 in 2004 (i.e., middle of the decreasing phase
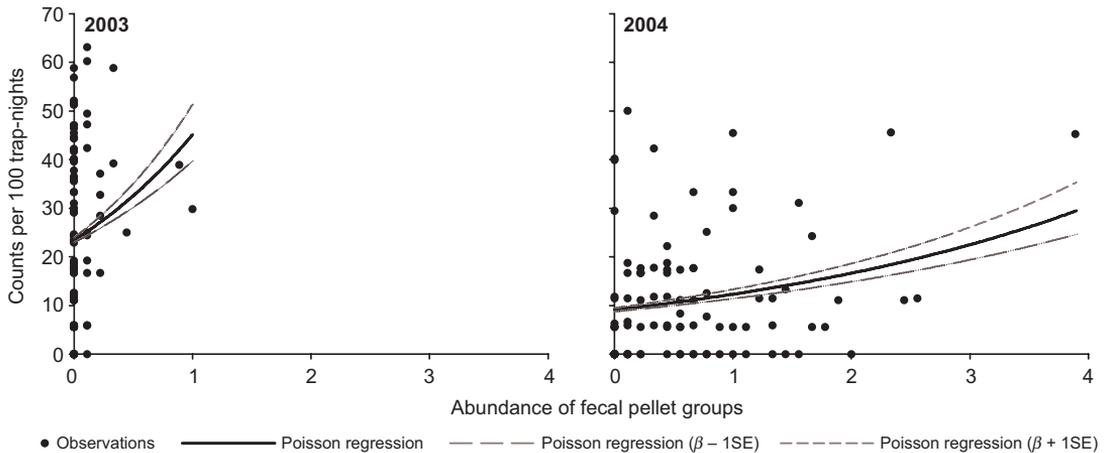
Fig. 2. Relationship between small rodent captures per 100 trap-nights and abundance of fecal pellet groups in 2003 (left) and 2004 (right). Solid black lines describe the Poisson regression between both variables while dashed grey lines refer to ± 1SE in coefficient estimates.

of the cycle) of which 404 (99%) and 187 (97%) were the southern red-backed vole (*Myodes gapperi*), corresponding respectively to 24.4 ± 1.8 and 11.3 ± 1.3 captures per 100 trap-nights. We are aware that all rodent species did not fluctuate in abundance synchronously to the red-backed vole, but as the latter represented the majority of captures, we did not distinguish between rodent abundance cycle and red-backed vole abundance cycle. Abundance of fecal pellet groups was of 0.05 ± 0.04 (SE) groups per plot in 2003 and of 0.63 ± 0.17 (SE) in 2004. Almost all (93%) pellet groups were representative of faeces of species belonging to *Myodes* (vole) genera according to characteristics proposed by Murie and Elbroch (2005), but identification to species could not be achieved. Considering the absolute dominance of the southern red-backed vole in harvest (*see* above), we assumed that fecal pellets originated from the same population of rodents.

GLMs with a Poisson error term showed similar results between years, with significant relationships between abundance of fecal pellet groups and captures per 100 trap-nights of small rodents (Fig. 2 and Table 1). Although these relationships were significant ($P < 0.0001$), they explained little of the variability in rodent captures per 100 trap-nights (pseudo-R^2 of 2.4% and 6.6% in 2003 and 2004, respectively). A large variability and the presence of several sampling grids with no rodent captures lead to over dispersed values in our datasets (Fig. 2). Finally, Taylor's log-log plots of mean abundance of fecal pellet group counts related to variance in those counts indicate that groups of fecal pellets are deposed in clumped patterns (Fig. 3). Significant relationships revealed by the GLMs suggested that variance increases linearly with mean counts of pellet groups (Table 2).

Table 1. Generalized linear models with a Poisson error term establishing a positive relationship between the abundance of fecal pellet groups (β_{pellet}) and small rodent captures per 100 trap-nights in 2003 and 2004 ($n = 100$ per year). β_0 refers to model intercept.

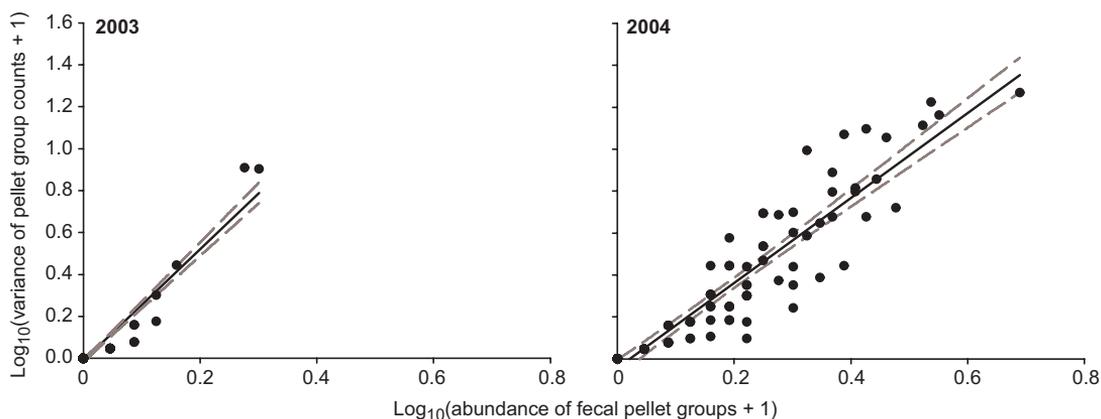| Year	Variable	Coefficient ± SE	Wald χ^2	P	Model pseudo-R^2
2003	β_0	3.155 ± 0.021	2299.70	< 0.0001	0.024
	β_{pellet}	0.655 ± 0.107	37.60	< 0.0001	
2004	β_0	2.210 ± 0.041	2850.95	< 0.0001	0.066
	β_{pellet}	0.301 ± 0.036	71.38	< 0.0001	

Fig. 3. Taylor's plot of the relationship between log-transformed abundance of fecal pellet groups and log variance of pellet group counts in 2003 (left) and 2004 (right). Solid black lines describe the linear relationship between both variables while dashed grey lines refer to 95% confidence intervals.

Discussion

Despite the fact that fecal pellet counts are currently used to predict relative abundances of several mammal species (*see* Gibbs 2000 for a review), our results suggest that no clear and strong relationship exists between the captures per 100 trap-nights of small rodents and the abundance of their fecal pellet groups in the eastern North American boreal black spruce forest. Although we statistically demonstrated the presence of a relationship between both indices, analyses and observations highlight the weakness of this relationship.

Such results support a previous experiment conducted by Hansson (1979) in Fennoscandian forests, who predicted that the strength of the relationship between rodent presence signs and relative abundance should increase if the rodent community is solely composed of one species. Although this was also the case in our study, red-

backed vole representing between 97 and 99% of our captures, it appears that using vole droppings as an abundance index is of limited reliability. Two factors may explain the lack of accuracy of the pellet-capture rodent relationship.

Firstly, rodent populations vary greatly in abundance, especially within season, but also within and between years. We thus consider that fecal pellet counts carried out in spring were not representative of mid-summer rodent captures per 100 trap-nights, as the late spring arrival of juveniles (Klemola *et al*. 2002) and the usual winter crash in abundance that follows the over-exploitation of winter food resources (Klemola *et al*. 2000) are two important sources of fluctuation in vole abundance. The time period when pellet counts allow for a higher predictability of abundance appears particularly short and seems limited to early spring, before the general increase in abundance observed in rodent populations from spring to autumn/winter (Hansson 1979,

Table 2. Generalized linear models establishing a positive linear relationship between the abundance of fecal pellet groups (β_{pellet}) and the variance in pellet counts in 2003 and 2004 ($n = 100$ per year). β_0 refers to model intercept.

Year	Variable	Coefficient ± SE	t	P	Model R^2
2003	β_0	−0.013 ± 0.005	−2.77	0.0067	0.907
	β_{pellet}	2.664 ± 0.086	30.83	< 0.0001	
2004	β_0	−0.043 ± 0.019	−2.22	0.0287	0.869
	β_{pellet}	2.026 ± 0.080	25.45	< 0.0001	

Petty 1999). This supports the observation by Pugh *et al*. (2003) that rodent abundances may be highly variable over a short period of time. Seasonal fluctuations in abundance can be induced by the important impact of predators on small rodents in the boreal forest (Korpimäki 1981, Hanski *et al*. 1991, 2001, Klemola *et al*. 2000) as well as the high fecundity of rodent populations (Desrosiers *et al*. 2002), resulting in rapid and large turnovers in abundance. Moreover, we noticed that the strength of the relationship between pellet counts and captured rodents did not change according to the phase of the rodent cycle. The 2003 data were collected during the upper phase of the rodent abundance cycle, while 2004's data were collected in the middle of the decreasing phase. Indeed, we found more rodent pellet groups in the decreasing phase of the rodent abundance cycle (i.e., 2004) than in the upper phase (i.e., 2003). Although we did not measure experimentally the decomposition rate of rodent pellets, this observation suggests that pellets may be able to persist on the boreal forest ground cover for a while (e.g., a common finding in snowshoe hare populations in North American boreal forests; *see* Prugh & Krebs 2004 or Murray *et al*. 2005 for examples). Moreover, we proposed the hypothesis that a relationship might exist between rodent diet and population levels and that if driven by density dependent effects, such a relationship could ultimately have an influence on fecal pellet persistence in the boreal forest. Whether such an index is unreliable or abundance fluctuations occur very rapidly, the observed relationships bring to light the low predictability of this approach.

Secondly, variance was seen to increase considerably with the number of pellet groups, as shown in Taylor's plot, suggesting that fecal pellet groups are deposited in clumped patterns and that their spatial distribution is highly heterogeneous. Although the decomposition rate of fecal pellets could differ spatially, we suggest that the rodent distribution in the environment is also driven by specific habitat requirements which lead to a heterogeneous rodent distribution and habitat use. Considering that rodent distribution and fecal pellet clumped patterns could both be habitat-mediated at a small spatial scale, such a strong variability in spatial arrangement could have dampened the relationship observed between droppings and captured rodents. Following Barnes (2001) who suggested that increases in variance of elephant droppings limits the reliability of using pellets as a reliable abundance estimator for this species, we consider that fecal pellet counts should be used at best as a sign of presence to analyze habitat use by voles.

Conclusions

Our results thus suggest that the rapid turnover of rodent populations may limit the use of pellet counts as an indirect estimator of abundance in mature boreal forest, at least when the rodent community is dominated by red-backed vole. Nevertheless, we consider that pellet counts may be a useful low cost and time efficient method of assessing recent habitat use by rodents, especially in situations where there is no precise indication of abundance, on a presence-absence basis. Indeed, using presence or absence to determine occupancy rate (MacKenzie *et al*. 2002) rather than absolute numbers can limit ambiguous interpretations and lead to more conservative conclusions on habitat use (MacKenzie 2005) through correlative evidence of the proportion of a habitat used by a given species (Zielinski & Stauffer 1996). This is especially true when numbers are very low (Stanley & Royle 2005), such as during the declining phase of the abundance cycle of red-backed vole. More precise estimations can be obtained by trapping or, if direct estimators cannot be used, by frequently (e.g. each month) monitoring several indirect estimators simultaneously (e.g. droppings, burrows, runways and clippings) as suggested by Hansson (1979) and Petty (1999). Consequently, we consider that fecal pellet group counting is an unreliable abundance estimator of rodents when used singly.

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