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Master of Science in Ecology

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Calibrating abundance indices of small rodents in sub-arctic tundra

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Abstract

Trophic interactions with vegetation and with avian and mammalian predators make small rodents key species of northern ecosystems. In order to get a better understanding of their role in these ecosystems accurate abundance measurement is required. In Fennoscandia, abundance indices obtained by snap-trapping in small quadrates have been one commonly used method for this purpose, although this method has not been calibrated against abundance estimates. The aim of this study was therefore to assess how captures from small quadrate snap-trapping of voles can provide reliable indices for population abundance, by calibration against abundance estimates obtained by capture-mark-recapture.

The study was conducted on the Varanger peninsula in Finnmark, northern Norway, with a main focus on the two dominant vole species in sub-arctic tundra: the root vole (*Microtus oeconomus*) and the grey-sided vole (*Clethrionomys rufocanus*). Root voles are known to be the dominant species in willow thickets and adjacent meadows, whereas grey-sided voles dominated in heath. Vole abundance was estimated using live trapping and capture-mark-recapture statistical models for closed populations in 20 grids (area 0.2 ha) based on four days of trapping in early and in late summer 2006. Snap-trapping was done immediately afterwards during two days. Linear models were used to calibrate abundance indices against estimates.

Habitat was the main variable affecting the relationship between indices and estimates: in meadows the index was about 2/3 of the estimated abundance, while in heath it was about 1/8. Other variables, including trapping period, age distribution and sex ratio, did not affect the calibration equations. The difference observed was likely due to species-specific capturability in live and snap-traps. Different calibration equations should be used for different habitats/species. The precision of the calibration equations was low and extending this study to higher vole densities and several trapping seasons would increase their accuracy. This study shows the importance of taking habitat and species-specific parameters into account when calibrating microtine indices.

Key words: calibration, snap-trapping, capture-mark-recapture, *Microtus oeconomus*, *Clethrionomys rufocanus*, tundra.

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Introduction

Small rodents and particularly microtines (voles and lemmings) are key species in many northern ecosystems as their cyclic fluctuations in population density have major impacts on the dynamics of their food plants and vertebrate predators (Steenseth and Ims 1993, Ims and Fuglei 2005). The causes of these fluctuations have been debated for over 80 years (Elton 1924, Gilg et al. 2003)), but there is still disagreement regarding the mechanisms that are necessary and sufficient for population cycles (e.g. Lambin et al. 2002). While some evidence suggests that trophic interactions - with microtines either as prey for carnivores (Gilg et al 2003) or as consumers of plants (Turchin and Batzli 2001) - are sufficient for inducing multiannual, periodic fluctuations, other plausible explanations have been proposed which might be better at explaining some of the known patterns (see e.g. Lambin et al. 2006 and Smith et al. 2006). The impacts of microtine fluctuations on the abundance of their vertebrate predators (such as rough-legged buzzard *(Buteo lagopus)*, least weasel *(Mustela nivalis)*, stoat *(Mustela erminea)* and Arctic fox *(Alopex lagopus)*) have been well documented (Elmhagen et al. 2000, Lambin et al. 2000, Sundell et al. 2004). It is therefore worrying that microtine dynamics seem to have changed in recent years, inducing a decline of some predators (Henttonen and Wallgren 2001, Ims and Fuglei 2005). The cause(s) of the changes in the cyclic fluctuations are unknown, even if indirect evidence suggests that recent climatic change might be one (Callaghan et al. 2004).

In order to quantitatively assess the role of microtines in ecosystems, reliable abundance estimation is essential. However, the use of abundance indices rather than absolute estimates, have often been considered to be sufficient for the evaluation of the variation in abundance of small rodents in space and in time (Hanski et al. 1994, Slade and Blair 2000). In fact, many of the best known time-series of microtine abundance are based only on indices and not on population abundance or density estimates (Henttonen et al. 1985, Hansen et al. 1999, Saitoh et al 2006). The use of indices to evaluate small-rodents populations has been justified for economical and practical reasons, but it has also been criticized, i.e. due to the assertion of equal capture probability, and scarcity of measurement of many crucial parameters (McKelvey and Pearson 2001, Conn et al. 2005). Despite this ongoing debate around the use of indices versus use of statistical modelling to evaluate population size, little is known about calibration of abundance indices. Such a calibration is necessary both in order to get quantitative estimates of ecosystem state (e.g. spring density and biomass of prey necessary

for predator breeding), and to achieve unbiased temporal comparisons in time or space (Yoccoz et al 2001).

In Fennoscandia, scientists have extensively used snap-traps, either placed in trap lines or quadrates (Myllymäki et al 1971, Hansson 1975). The latter, with three snap-traps located in each corner of a 15m side quadrate, has the advantages of being easy to implement in fragmented and heterogeneous habitats and seems to work well for different microtine species: *Microtus, Arvicola* and *Clethrionomys* spp. (Myllymäki et al. 1971). The small quadrate method was also constructed to avoid trap saturation, i.e. a lower capture rate at high densities (Henttonen et al. 1987, Xia and Boonstra 1992, Hanski et al. 1994).

The aim of this study was therefore to calibrate indices from small-quadrate snap-trapping against abundance estimates obtained on the basis of live trapping and capture-mark-recapture (CMR) statistical methods (Nichols and Pollock 1983, Lee and Chao 1994). Statistical modelling of CMR data is assumed to provide a better estimate of abundance, in the sense of having known statistical properties, rather than other abundance indices such as Minimum Number Alive (MNA; see e.g. Jolly and Dickson 1983). CMR statistical modelling is an approach commonly used to estimate population size of animal species in general (Nichols 1992). It is preferable to several enumeration estimators which rely on the unlikely assumption of a constant probability of capture, equal or close to 1 (Nichols and Pollock 1983). CMR modelling relies on estimating capture probability, p, and derives the estimated population size based on: $N = N_{capt} / p$, where N is population size and N_{capt} the number of captured individuals. Models for estimating p are based on different assumptions regarding factors influencing capture probability. These factors are usually considered under three main headings: time (variability among capture sessions), individual heterogeneity and behavioural response to capture (Darroch 1958, Otis et al. 1978, White et al. 1982, Seber 1986). Individual heterogeneity is often the most serious source of bias in small rodent populations (Parmenter et al 2003, Conn et al 2006).

This study focus on the abundance of the two dominant microtine species in sub-arctic habitats on the Varanger peninsula in northern Norway: the grey-sided vole *(Clethrionomys rufocanus)* and the root vole *(Microtus oeconomus).* As population structure can influence capturability, trapping was done in two periods; during early summer when most individuals belong to overwintering cohorts, and during late summer when the young-of-the-year are trappable.

Material and methods

Study Area

The fieldwork took place on Båtsfjordfjellet and Kongsfjordfjellet on the Varanger peninsula in northeastern Finnmark, 70ºN 29ºE during two weeks: the 17-23rd of July and 4-10th of September, 2006. According to measurements by the Norwegian Meterological Institute (www.met.no) at different stations located around the Varanger peninsula, the average annual temperature on the peninsula is 1.0-1.5ºC and the annual precipitation is 650-675 mm (for further details and weather stations see www.met.no). In 2006 the annual precipitation increased above normal to 700-1000 mm. The study area belongs to the low alpine/sub-arctic tundra which lies above the tree-line and is dominated by cold-tolerant plants such as mosses (*Bryophyta* spp. and *Marchantiophyta* spp.), sedges (*Cyperaceae* spp.), lichens and low-growing shrubs (e.g. juniper (*Juniperus communis*) and dwarf birch (*Betula nana*)), willows (*Salix spp.*) and dwarf-shrub heath (e.g. *Vaccinium spp.* and *Empetrum hermaphroditum*) (Killengreen et al. 2007). Typical mammal species living in the low alpine/sub-arctic are Norwegian lemmings (*Lemmus lemmus*), grey-sided voles (*Clethrionomys rufocanus*), root voles (*Microtus oeconomus*), least weasels (*Mustela nivalis*), stoat (*Mustela erminea*) and semi-domesticated reindeer (*Rangifer tarandus*).

The study grids were located at 130-250 m. a.s.l. within a distance of 40 kilometres (Figure 1). Trapping grids were distributed in two vegetation strata (Figure 2). The first was typical of the habitat of grey-sided voles –heath with extensive dwarf-shrub vegetation, particularly bilberries (*Vaccinium myrtillus*) (Ims 1987, Johansson and Ims 1990). The second included the habitat of root voles and Norwegian lemmings –mires/moist meadows with willow thickets (Johansson and Ims 1990, Hole and Waldeland 2002).
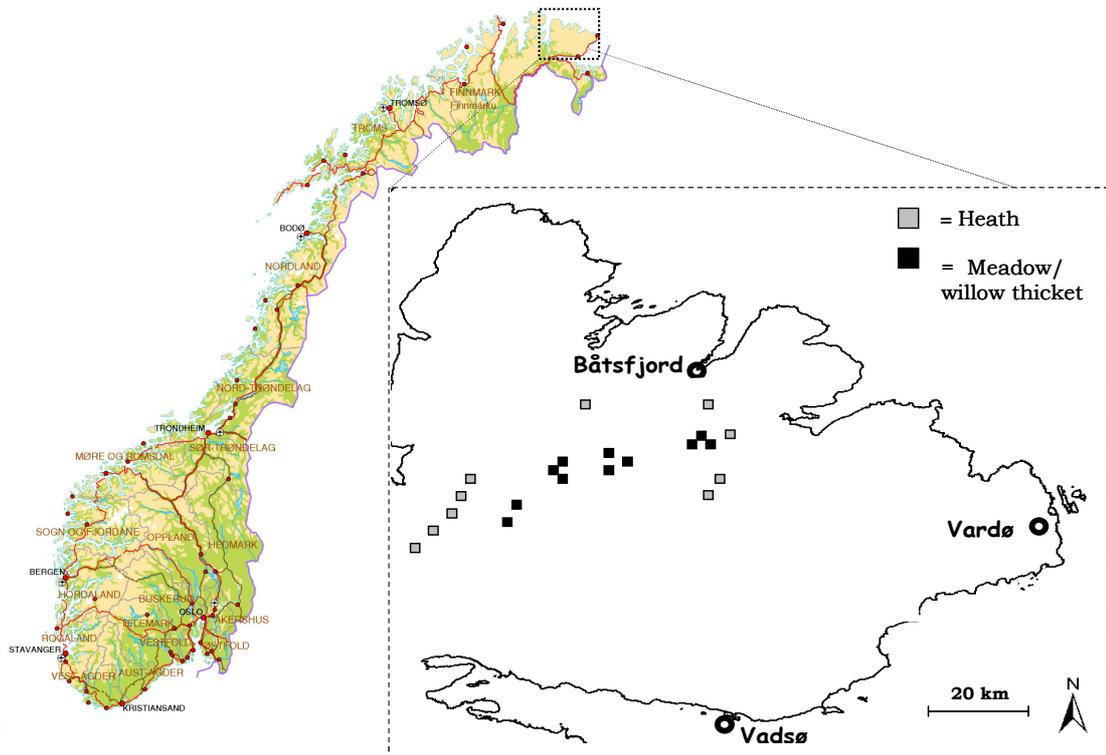
Figure 1: Study area on the Varanger Peninsula with 10 grids in heath (grey squares) and 10 grids in meadow (black squares).

Figure 2: Heath (left), main habitat of grey-sided vole, and willow thicket/moist meadow (right), main habitat of root vole.

Study design

Live trapping was done for three days in 10 grids in heath and 10 grids in willow/meadow, and then immediately followed by snap-trapping for two days in the same plots. The two periods of trapping resulted in 20 replicates for each type of habitat. All traps were checked once a day during the trapping period.

Trapping grid

Live-trapping grids consisted of 16 traps with a 15 m distance between traps (area = 0.2 ha) and were designed to encompass the snap-trapping area (Figure 3). The snap-trapping followed Myllymäki's small quadrate removal design (Myllymäki et al 1971), and consisted of 12 traps distributed on the four trapping stations in the middle of the live-trapping grid, each with three snap-traps inside a radius of 2 m from the corners of the small quadrate (area = 0.02 ha). The snap-trapping grids in the willow/meadow habitat were located 1 m inside the thicket edge with the rest extending into the meadow. The live-trapping grids were therefore placed with the innermost row of traps around 15 m inside the thicket or on the other side if the thicket was narrow (Figure 3). Individual voles were marked individually by toe clipping. Species, sex, weight and reproductive status were recorded. Functional category (adult and subadult/juveniles) was decided on the basis of individual weight; i.e., adults as grey-sided vole $\geq$ 25g, and for root vole adults $\geq$ 30g (Yoccoz and Ims 2004).

Traps

The live traps were of type Ugglan special nr 1 (Figure 4), and may capture more than one individual (Henttonen et al. 1997, Lambin et al. 2000). They were baited with potatoes and oats and the trapping was conducted for 72 hours, giving 3 nights x 16 traps = 48 trap nights in each grid and each period. The snap-traps were of type Rapp (Figure 4). Each trap was fastened with a thread and a nail, and raisins and oatmeal were used as bait. The snap-traps were set for 48 h and checked twice, each quadrate then representing 2 nights x 12 traps = 24 trap nights (Ekerholm et al. 2004). Live traps and snap-traps were situated in places bearing recent signs of animals, i.e. holes, tracks, fresh dropping and fresh heaps of grass clippings.
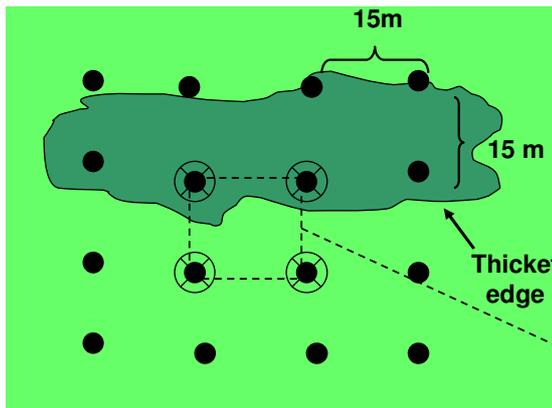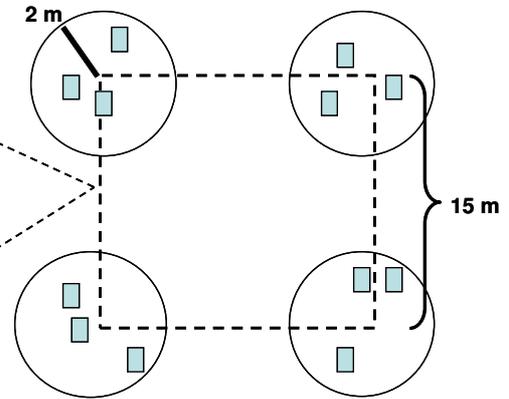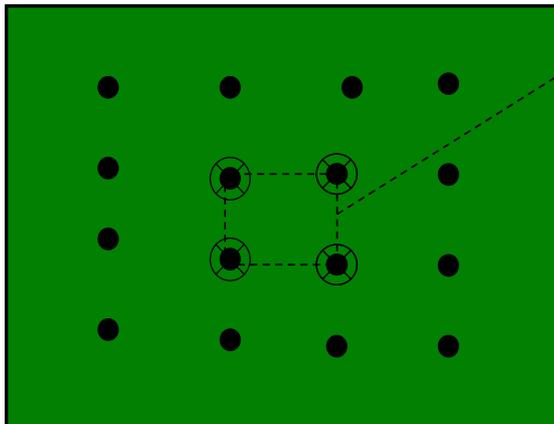
Figure 3: Trapping grids in meadow (upper left) and heath (lower left) with examples of snap trapping in small quadrates.

Figure 4: Snap-trapping (left) and live-trapping (right).

Estimating population abundance by Capture-Mark-Recapture analysis

Live-trapping took place over three days (the traps were set on the first day and checked over the next two days). It was assumed that change in population size over this time period was small enough for the assumption of closure (no births, deaths, emigrants or immigrants) to be a reasonable approximation, and the effects of violating that assumption were minimal (Otis et al. 1978). The different capture-recapture models for closed populations allow for various causes of variation in capture probability; time effects, behavioural response to capture and individual heterogeneity (Otis et al. 1978, White et al. 1982).

- In model M_t, (t = time), capture probabilities vary between capture sessions (days), for example due to varying weather conditions.

- In model M_b, (b = behavioural) initial capture affects the capture probability on subsequent occasions. This means that an animal could, after the first capture, become either "trap happy" or "trap shy". The model assumes that on any trapping occasion, all unmarked animals have a different probability of capture than marked animals.

- Model M_h (h = heterogeneity) assumes that each animal has its own unique capture probability, p_1, p_2,..,p_N, independent of the other members of the population, and the capture probability of each animal is constant over all trapping occasions. Heterogeneity is expected in all natural populations.

- Model M_{th} combines time and heterogeneity effects, assuming a multiplicative form of the effects.

Other combinations were not used (such as model M_{bh}, M_{tb}, or M_{tbh}) since the relatively small sample size (both in terms of number of individuals and capture session), did not warrant the use of more complicated models. Moreover, models including heterogeneity have often been discussed as the most robust (Burnham and Overton 1978, Conn et al. 2006).

Different estimators have recently been proposed for the same models in order to reduce bias and increase precision. One of these is the non-parametric sample coverage approach modified by Lee and Chao (1994) for models M_h and M_{th}, which assumes that the heterogeneity effects can be summarized in terms of the mean and coefficient of variation (CV) of p_1, p_2, ...,p_N. The CV is zero if the animals are equally capturable, and the larger the CV the greater degree of heterogeneity among animals. The jackknife estimator is another approach that has been widely used for the model M_h, and has been proven to give low bias

and robust abundance estimates (Burnham and Overton 1978, Manning et al. 1995). Population abundance estimates based on individual capture history were calculated using program CARE-2 (Chao an Huggins 2005) and four different closed population CMR-models; model M_h with a sample coverage approach, model M_h with the second order jackknife estimator, model M_h with the interpolated jackknife estimator and the model M_{th} with a sample coverage approach.

Statistical analysis

Linear models were used to analyse the relationship between the abundance indices based on snap-trapping and the abundance estimates based on live trapping and CMR modelling. Calibration studies usually rely upon known population values (i.e. without errors) and observed index values. The calibration equations are then based on regressing the abundance indices on the known values with calibration equations inverting these regressions in order to predict population values from the indices. A similar approach was used here even if the exact abundance was estimated and not known, setting the number of animals in snap-traps as the response variable, with abundance estimate as the predictor variable. Distinctions in trapping success between species or periods could then be analyzed. Age distribution and sex-ratio were included as covariates in the model to see if these demographic parameters affected capture probability in the snap-traps. To select the best model and to determine what variables fitted the data best I used Akaike`s Information Criterion (Akaike 1973) with a correction term for small sample size (AIC_c) (Anderson and Burnham 2002). When the difference in AIC_c between two models was less than 1, the simplest model was chosen according to the principle of parsimony (Burnham et al. 1995, Anderson and Burnham 2002). Because of the dissimilar sample area of live trapping and snap-trapping, equivalence between indices and estimates was not expected.

An analysis of the effects of other species (i.e. shrews) on capture rates in live traps was also done by linear modelling. Capture rate in each grid were calculated by number of animals in live traps divided by abundance estimates. The statistical analyses were done in R (R Development Core Team, 2006).

Results

Trapping

In total 383 small mammals were trapped; 142 grey-sided voles, 147 shrews, 88 root voles and 6 lemmings (Table 1). Habitats were confounded with species, with mainly root voles captured in meadow, and only grey- sided voles captured in heath. More animals were captured with live traps than with snap-traps in heath, but the reverse was true in meadows (Table 1and Figure 5).In meadows more animals were captured in live traps the second and third day than the first day of trapping in both periods, while in heath there was no such pattern during the three days of live-trapping. The majority of shrews were captured in live traps in meadows and most of them died in the traps. The capture in snap-traps where about equal for both species ($n_{grey\text{-}sided\ vole}$=66 and $n_{root\ vole}$= 67), and all the lemmings captured were taken in snap-traps. Among the animals first captured by live traps, there were about the same recapture rate in snap-traps in both habitats (Table 1). The number of animals caught increased from July to September. This increase was particularly large for shrews, but less for voles.

Table 1: Number of animals captured in live traps and snap-traps. "R"= Root vole, "GS"=Grey-sided vole, "% marked" is the percentage of the total number of animals in snap-traps that are marked, "% recaptured" is the percentage of the animals captured and marked in live traps that were recaptured in snap-traps.

| | | Live trapping | | | Snap-trapping | | | | | | | | | % | % |
| | | | | | Marked | | Unmarked | | | | Total | | | | |
Habitat	Period	R	GS	Shrews	R	GS	R	GS	R	GS	Shrews	Lemming		marked	recaptured
Heath	July	1	40	3	0	16	0	8	0	24	0	0		67 %	39 %
Heath	Sept	1	59	12	*0*	*25*	*0*	*10*	*0*	*35*	*1*	*2*		*71 %*	42 %
Heath	*Total*	*2*	*99*	*15*	*0*	*41*	*0*	*18*	*0*	*59*	*1*	*2*		*69 %*	*41 %*
Meadow	July	12	7	20	7	5	16	0	23	5	0	3		43 %	63 %
Meadow	Sept	22	9	119	10	1	34	1	44	2	4	1		24 %	35 %
Meadow	*Total*	*34*	*16*	*139*	*17*	*6*	*50*	*1*	*67*	*7*	*4*	*4*		*31 %*	*46 %*
Total		36	115	154	17	47	50	19	67	66	5	6		48 %	42 %
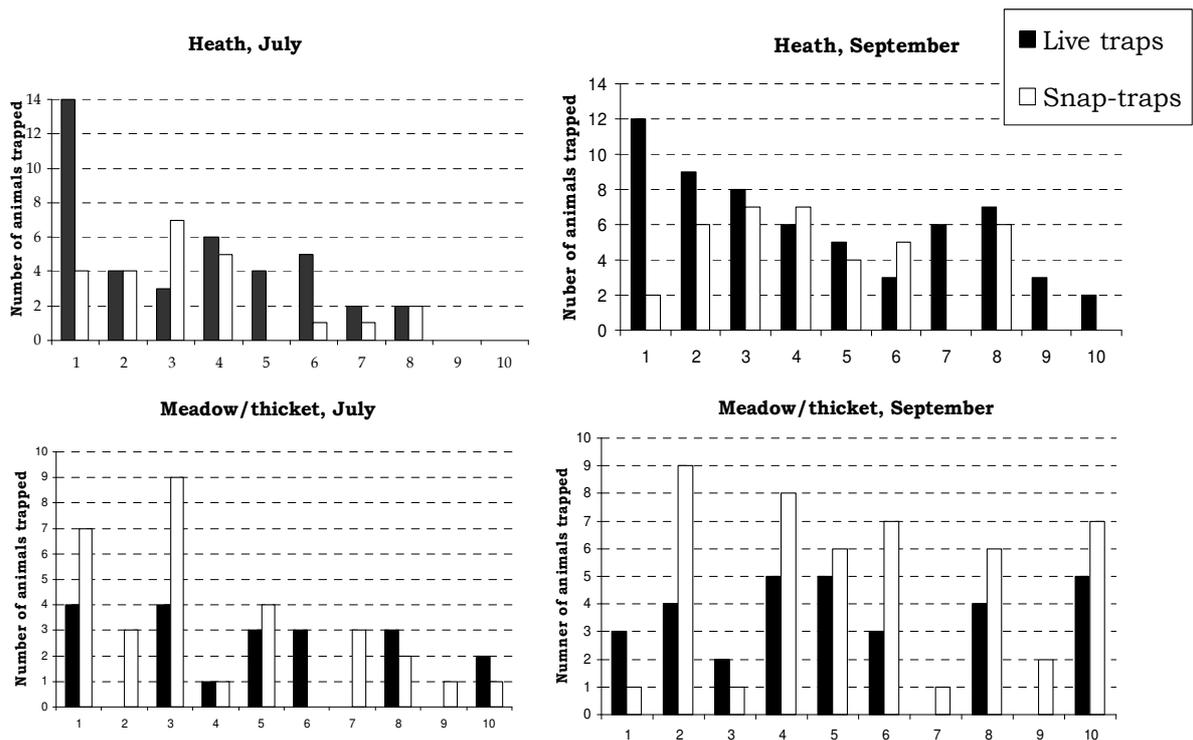
Figure 5: Number of animals trapped with live traps and snap-traps in each grid (1-10) in heath and meadow in July and September. Note the higher capture rate with live traps than snap-traps in heath, and the opposite result in meadow.

More adults than juveniles were caught in both trap types. During July, 68% - 87% of the individuals caught in snap-traps and 75% - 79 % of those in live traps were adults. During September, 65% - 85% of the captured animals in snap-traps and 48% - 58% of the animals in live traps were adults. More adults than juveniles were caught in the meadow compared to the heath (Appendix 1). The sex ratio was in general close to 50 %, however in the heath, 56 – 60% of the animals caught in snap-traps were males (Appendix 1).

Focusing on the sample coverage of snap-traps, among the 47 grey-sided voles captured in both trap types, 37 were captured with live traps outside the small quadrate before they were snap-trapped, while 10 were trapped inside the small quadrate with both trap types. Of the 17 tundra voles captured in both trap types, 8 were captured in live traps inside and 9 outside the small quadrate before they were snap-trapped, indicating a smaller sampling coverage by snap-traps in meadows than in heath.

Abundance estimates

The estimated abundances were higher in heath than in meadow. One trapping grid in heath had particularly high estimates with between 13.6-18.2 and 20.8-24.8 animals during July and September respectively (grid number 1 in Figure 6). In general Model M_h(SC2) gave the

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lowest estimates while $M_h(JK_2)$ gave the highest. Because of the high similarity among models, the model Mh with the second order jackknife estimator, $M_h(JK_2)$, was chosen for further analysis. This is a commonly used model, and has been proven to give low bias and robust abundance estimates (Burnham and Overton 1978). All abundance estimates with standard errors and confidence intervals are given in Appendix 2.
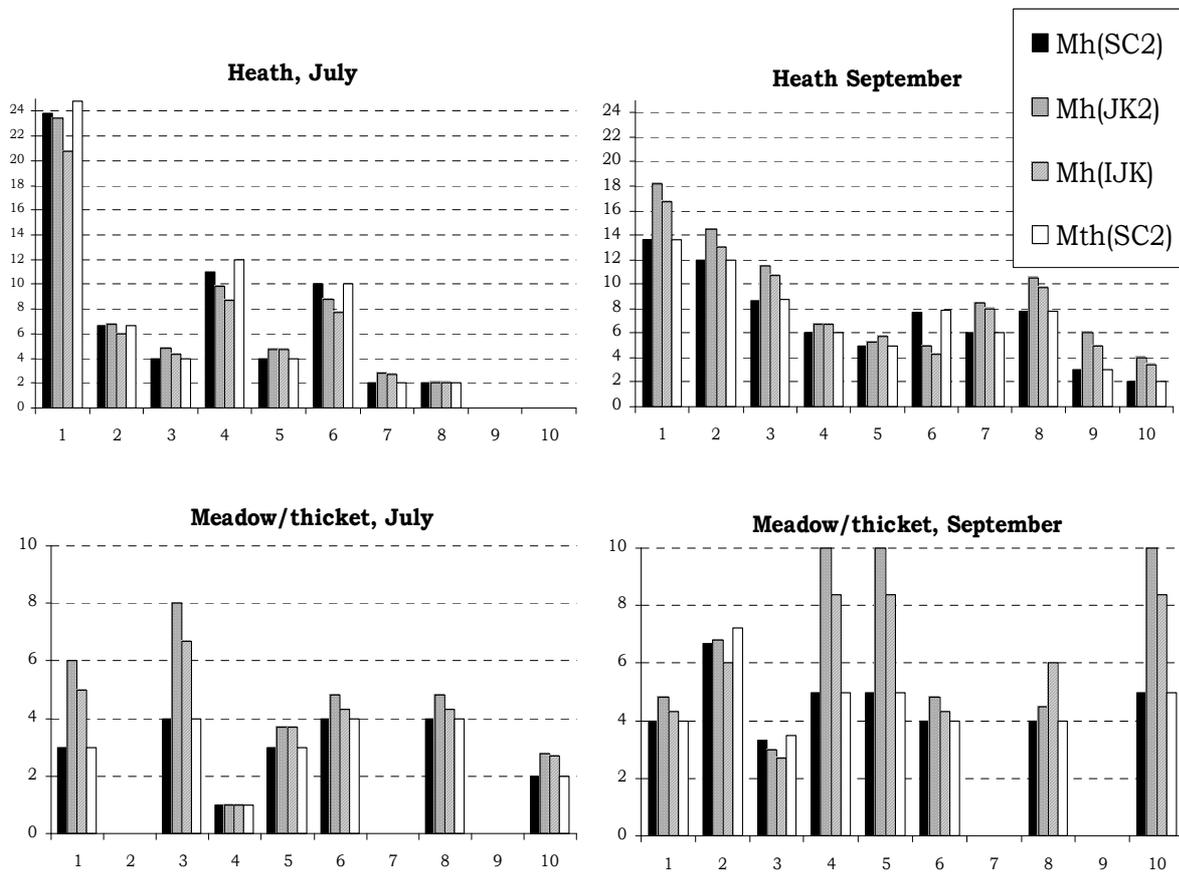
Figure 6: Abundance estimates in each grid (1-10) in the two habitats in July and September from four different closed capture-mark-recapture models: Mh(SC2), includes heterogeneity with the sampling coverage approach. Mh(JK2) includes heterogeneity with the jackknife estimator. Mh(IJK) includes heterogeneity with the interpolated jackknife estimator. Mth (SC2) includes effect of time and heterogeneity with the sampling coverage approach.

Impact of shrews on capture rates

Because of the large amount of shrews in live traps (139 in meadow and 39 in heath) their potential impact on the vole capture rate in live traps was analysed, expecting the capture rate in live traps to decrease with increasing numbers of shrews. The linear model "capture rate in meadow" ~ "number of shrews in live traps" gave no evidence for such an effect ($R^2 = 0.036$, p-value = 0.42.

Comparison of captures in snap-traps and abundance estimates

The selected linear regression model included habitat and interaction between density estimate and habitat as predictors with $R^2 = 0.364$ and P = 0.008 (Appendix 3). There were small differences in AICc (ΔAICc = 0.002) between this model and the model including sex, habitat and interaction among habitat and abundance estimates, but the former model was chosen due to its simplicity. The result from regression modelling indicates that the relationship between numbers of animals captured in snap-traps and estimated population size from live traps differences among type of habitat. There is also an interaction between the estimates and habitat, leading to a dissimilar relation between the estimates and abundance index in the two habitats; while the abundance index was about 2/3 of the estimated abundance in meadow, it was about 1/8 in heath.

With the use of this linear model, a calibration equation was constructed for each habitat type. The captures in snap-traps could then be used to calculate the estimated population abundance with this equation (Figure 7). .In meadow, the equation for the regression line ($R^2 = 0.515$) with standard errors is:

Estimated abundance N $_{Meadow}$ = (N $_{snap\text{-}traps}$ / 0.638 ± 0.146) + 1.239 ± 0.79

In heath the equation for the regression line ($R^2 = 0.134$) with standard errors is:

Estimated abundance N $_{Heath}$ = (N $_{Snap\text{-}traps}$ / 0.1693 ± 0.10) + 1.751 ± 0.97
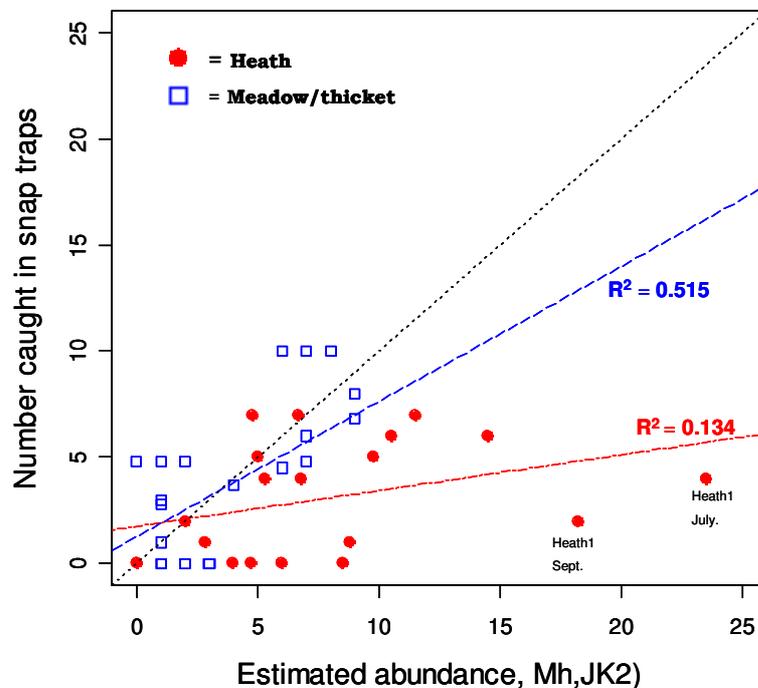
Figure 7: Regression between number of animals captured in snap-traps and abundance estimates. Blue squares and stippled line indicates meadow, red circles and solid line indicates heath. Black, dotted line shows the equivalence line.

The two trapping grids in heath (Heath1 in July and September, marked in Figure 7) with large abundance estimates but few animals caught in snap-traps had a significant effect on the regression parameters and decreased the fraction of variation explained by the regression. When removing these two plots from the regression analysis, the new correlation coefficient R^2 for the model ($N_{snap-traps} \sim Mh_{JK2}$ + Habitat + (Mh_{JK2} : Habitat)) is 0.445, and the correlation coefficient in heath separately have increased with 0.189 (Figure 8). The new equation for the regression line in heath with standard errors is then:

Estimated abundance, N_{Heath} = ($N_{Snap-traps}$ / 0.4166 ± 0.15) + 0.4703 ± 1.096
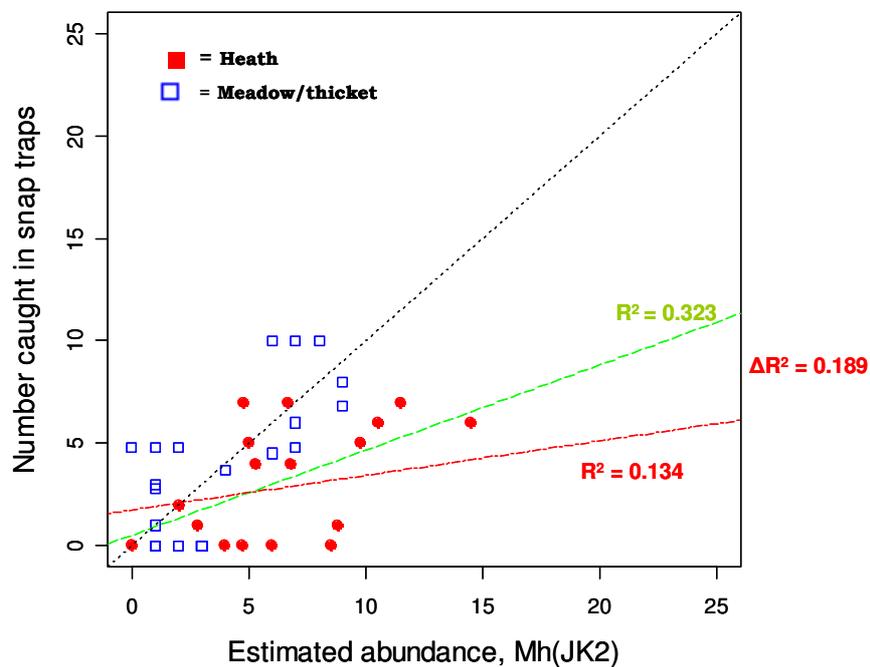
Figure 8: Regression between number of animals captured in snap-traps and abundance estimates. Two outliers (grids in heath) are removed from the figure. Blue squares indicate grids in meadow, red circles indicate heath. Green stippled line indicates the new regression line without outliers, red solid line indicates regression line with outliers (the black, dotted line shows the equivalence line).

Including period as a covariate in the linear regression model caused the AICc-value to increase by 2.0. Hence, we do not need to consider what period the trapping takes place. Neither sex ratio nor age distribution in the live trapped population gave lower AICc values.

Discussion

Assessing abundance is essential in understanding the role of microtines in northern ecosystems, and snap-trapping in small quadrates has been commonly used in Fennoscandia for this purpose. Evaluating the proportionality of indices obtained using snap-trapping and abundance estimates was the principal objective in this study and this was done through estimating calibration equations of small quadrate snap-trapping indices against capture-mark-recapture abundance estimates. Different equations were obtained in root vole habitat (moist meadow/willow thicket) and grey-sided vole habitat (heath). In meadow/willow thicket the abundance index was about 2/3 of the estimated abundance and in heath it was about 1/8 or 1/3 depending on the inclusion of two outlying population estimates. There was no evidence that the period during which the trapping took place, the age distribution and the sex ratio, did affect the calibration equations.

The difference in calibration equations among habitats is most likely due to unequal species-specific capturability in snap-traps and live traps. The larger number of grey-sided voles than root voles in live traps compared to snap-traps reflects the dissimilar capturability of the two species. *Microtus* spp. (including root voles) and *Clethrionomys* spp. (including grey-sided voles) differ both behaviourally and demographically (Viitala and Hoffmeyer 1985, Stenseth et al. 1998, Ylönen et al. 1990) and some of these differences could explain their different capturability. For example, *Clethrionomys* spp. and *Microtus* spp. do not share the same food preferences; while *Clethrionomys* spp. have a variable diet, with a preference for shrubs such as bilberry, *Microtus* spp. prefer graminoids (Stenseth et al. 1988). The use of different baits in the two trap types, could therefore partly explain the different capturability among species; potatoes and oats may not be preferred by root voles, while oatmeal and raisins may be preferred by both species.

The absence of pre-baiting in this study may also to some extent explain different capturability among species. Pre-baiting traps has often been argued to be an essential step in attracting animals to live traps (Eccard and Ylönen 2001, Graham and Lambin 2002, Korpimaki et al.), and could account for different capture rates among species (Chitty and Kempson 1949). In the present study, the numbers of root voles increased gradually with time, while no such pattern was found in grey-sided vole captures. Consequently, it is possible that root voles were showing a behavioural response to trapping and needed time to

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get accustomed to the unknown objects in their habitat before entering the traps, while the grey-sided voles did not. This corresponds to the results of other studies done on *Microtus* spp. showing a similar behavioural pattern, often described as "trap-happiness" (Yoccoz et al 1993). Pre-baiting traps and increasing the number of days of live-trapping could therefore be considered as methods to potentially adjust for these behavioural differences among species and improve abundance estimates.

Comparison studies of snap-traps versus live traps have resulted in different conclusions depending on the species, sampling design and sample size. For instance (Cockrum 1947) concluded that live trapping provides a much more reliable index of population density than snap-trapping, while (Wiener and Smith 1972) argued that live trapping might not be as efficient as snap-traps. Hansson and Hoffmeyer (1973) studied index trapping of different species (including *Microtus agrestis* and *Clethrionomys glareolus*) in small quadrates with either snap-traps or live traps, and suggested that the trapping efficiency depends on the species as well as the time of year during which the trapping takes place, but this conclusion was valid mainly for *Apodemus* and *Sorex*. Their paper did not provide detailed information for *M. agrestis* or *C. glareolus* that could be used in this study. However, as mention earlier, we did not find evidence for any effect of period, age distribution nor sex ratio on the calibration equations.

Even though age distribution had no significant impact on the calibration equations, the majority of adults in both trap types could influence the number of captures in other phases of the population density cycle. The adult-juvenile ratio was larger in snap-traps than in live traps (77% in snap-traps and 61% in live traps) with largest difference in meadow grids. While there are in general more juveniles representing the population in the increasing phase of the cycle, and less in the decreasing phase (Krebs and Myers, 1974), the number of animals caught could as a consequence be lower in the increasing phase. Hence the distinction in juvenile/adult ratio among habitats could have an impact on the calibration equations in other phases of the population cycle.

As well as the calibration equations are dependent on the dissimilar captures in snap-traps and live traps, the abundance estimates are also involved in the linear models, and could take part in explaining some of the differences among habitats. There was little variance among the abundance estimates obtained by the different closed population models. However, the variance among the different grids was relatively large. One of the trapping grids in the heath habitat had particularly high estimates compared to the others; when this grid was

removed from the regression analysis, the regression coefficient changed considerably. This grid had no particular large capture in snap-traps (four animals in July and two in September). The high abundance estimate could be attributed to a large number of single captures in live traps (i.e. few recaptures), but the reason for few captures in snap-traps in this special grid was unclear. The large variance among grids, particularly in heath, will increase the confidence intervals and standard errors of the abundance estimates, whereas larger sample size will very likely improve their precision. Spatial variation within study areas could evidently be a problem in this kind of calibration studies. Therefore, in order to get more precise calibration equations, one should use larger sample sizes.

The area coverage of traps is essential in calculating population density (i.e. abundance divided by the effective trapping area), and this study was designed to examine the relationship between the snap-trapping small quadrates and live-trapping grids encompassing the small quadrates. There are two issues regarding area coverage: i) the effective trapping area of snap-trapping quadrates, and ii) the effective trapping area of the live trapping grids. Although the sample size with live traps in the meadow was relatively low, with only 17 animals, a tendency of smaller effective trapping area by snap-traps in meadows than in heath could be assumed by the recaptured animals in snap-traps. Among the animals captured with snap-traps in the small quadrate, 78% of the grey-sided voles and 52% of the root voles were captured with live traps outside the small quadrate before they were snap-trapped. This result could arise from snap-traps being more attractive to grey-sided voles than to root voles, or the dissimilar spatial use among the two species. Generally *Clethrionomys* spp. have larger home ranges than *Microtus* spp. (Stenseth et al. 1988), and thereby could have a greater chance of running into a trap. If the snap-traps cover larger areas in heath than in meadow, the result could be an overestimated abundance in heath or underestimation in meadow. This result emphasizes the dissimilarity among habitats and the importance of using different calibration equations in the two habitats, as done in this study.

Regarding the effective trapping area of live trapping grids (i.e. what is used to estimate true density and which include the area covered by live traps, 0.2 ha, and an additional edge), it will depend on the spatial use of the trappable population (Efford 2004) as well as the heterogeneity of the habitat. Larger live trapping grids with a smaller relative edge effect would have included other habitats than the two that are focused on in this study and would have negated the advantage of using habitat specific small quadrates. This study provides therefore a first step for calibrating small quadrate trapping indices, by indicating correlation

among indices and estimates and emphasizing specie-specific parameters, but a fuller calibration approach may require additional knowledge of space use of the two species dominating sub-arctic ecosystems on Varanger peninsula (e.g. Ims1987, Bjørnstad et al. 1998).

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Appendix 1: Age distribution and sex ratio.

Age distribution

		Live traps			Snap-traps		
Habitat	**Period**	**Number of animals**	**Number of adults**	**Percentage adults**	**Number of animals**	**Number of adults**	**Percentage adults**
Heath	July	40	30	75 %	25	17	68 %
Heath	September	61	29	48 %	37	24	65 %
Heath	**Total**	**101**	**59**	**58 %**	**62**	**41**	**66 %**
Meadow	July	19	15	79 %	31	27	87 %
Meadow	September	31	18	58 %	48	41	85 %
Meadow	**Total**	**50**	**33**	**66 %**	**79**	**68**	**86 %**
TOTAL		**151**	**92**	**61 %**	**141**	**109**	**77 %**

Sex ratio

		Live traps			Snap-traps		
Habitat	**Period**	**Number of animals**	**Number of males**	**Percentage males**	**Number of animals**	**Number of males**	**Percentage males**
Heath	July	40	22	55 %	25	14	56 %
Heath	September	61	29	48 %	37	22	60 %
Heath	**Total**	**101**	**51**	**50 %**	**62**	**36**	**58 %**
Meadow	July	19	9	47 %	31	17	55 %
Meadow	September	31	17	55 %	48	24	50 %
Meadow	**Total**	**50**	**26**	**52 %**	**79**	**41**	**52 %**
TOTAL		**151**	**77**	**51 %**	**141**	**77**	**55 %**

Appendix 2 Abundance estimates

Habitat	Period	Model with heterogeneity (Sample coverage)					Modell with heterogeneity (Jackknife)					Model with heterogeneity (interpolated jackknife)					Model with heterogeneity and time (Sampling coverage)				
		Estimate	Bootstrap SE	Asymptotic SE	95%CI (log-transf.)	95%CI (percentile)	Estimate	Bootstrap SE	Asymptotic SE	95%CI (log-transf.)	95%CI (percentile)	Estimate	Bootstrap SE	Asymptotic SE	95%CI (log-transf.)	95%CI (percentile)	Estimate	Bootstrap SE	Asymptotic SE	95%CI (log-transf.)	95%CI (percentile)
Heath1	July	23.8	23.77	11.76	(14.7,163.0)	(14.0,88.7)	23.5	4.55	4.43	(17.9,37.2)	(18.33,28.50)	20.8	3.34	3.39	(16.74,30.9)	(17.3,24.2)	24.8	31.31	12.44	(14.6,217.1)	(14.0,108.6)
Heath1	Sept	13.6	5.92	3.54	(12.1,51.8)	(12.0,28.0)	18.2	3.65	3.65	(14.1,30.0)	(14.0,22.67)	16.7	2.59	2.79	(13.69,24.9)	(14.0,19.5)	13.6	6.51	3.54	(12.1,56.2)	(12.0,32.83)
Heath2	July	6.7	2.7	5.08	(4.5,17.8)	(4.0,12.0)	6.8	2.2	2.42	(4.7,14.9)	(4.50,9.0)	6	1.85	1.83	(4.43,13.3)	(4.0,7.4)	6.7	2.7	5.08	(4.5,17.8)	(4.0,12.0)
Heath2	Sept	12	7.17	4.69	(9.2,53.9)	(9.0,35.6)	14.5	3.24	3.4	(10.9,25.0)	(11.0,18.67)	13	2.55	2.59	(10.28,21.5)	(11.0,15.2)	12	8.37	4.69	(9.2,62.9)	(9.0,38.25)
Heath3	July	4	1.48	2.71	(3.12,11.3)	(3.0,5.7)	4.8	1.74	1.96	(3.4,11.8)	(3.0,7.0)	4.3	1.4	1.49	(3.25,10.2)	(3.0,5.7)	4	1.65	2.71	(3.1,12.4)	(3.0,5.67)
Heath3	Sept	8.7	6.23	2.15	(8.0,50.2)	(8.0,24.0)	11.5	2.63	2.75	(8.9,21.0)	(8.33,14.83)	10.7	1.93	2.11	(8.75,17.5)	(8.6,12.8)	8.8	8.64	3.31	(8.0,66.1)	(8.0,31.0)
Heath4	July	11	10.07	7.67	(6.4,66.6)	(6.0,44.0)	9.8	2.58	2.8	(7.2,18.7)	(6.67,13.0)	8.7	1.84	2.12	(6.80,15.1)	(6.6,10.7)	12	15.5	9.24	(6.4,104.5)	(6.0,58.70)
Heath4	Sept	6	0.83	0.1	(6.0,6.0)	(6.0,8.33)	6.7	0.86	1.31	(6.1,10.6)	(6.0,8.83)	6.7	0.61	1.05	(6.14,9.1)	(6.0,8.0)	6	2.22	0.1	(6.0,6.0)	(6.0,8.90)
Heath5	July	4	1.14	0	(4.0,4.0)	(4.0,6.67)	4.7	0.84	1.31	(4.1,8.5)	(4.0,6.83)	4.7	0.57	1.05	(4.16,6.8)	(4.0,6.0)	4	1.93	0	(4.0,4.0)	(4.0,10.0)
Heath5	Sept	5	0.46	0	(5.0,5.0)	(5.0,5.83)	5.3	0.78	1.2	(5.0,9.8)	(5.0,7.67)	5.7	0.58	1.05	(5.15,7.9)	(5.0,7.0)	5	0.96	0	(5.0,5.0)	(5.0,6.05)
Heath6	July	10	4.81	8.1	(6.0,29.4)	(5.0,16.67)	8.8	2.57	2.8	(6.2,17.6)	(5.8,11.83)	7.7	1.95	2.13	(5.76,14.6)	(5.67,9.1)	10	5.98	8.1	(5.8,36.7)	(5.0,21.91)
Heath6	Sept	7.7	5.53	7.63	(3.7,32.2)	(3.0,20.33)	5	2.11	2	(3.4,13.9)	(3.0,7.0)	4.3	1.42	1.49	(3.24,10.3)	(3.0,5.7)	7.9	6.21	8.31	(3.7,36.3)	(3.0,23.67)
Heath7	July	2	0	0.94	(2.0,2.0)	(2.0,2.0)	2.8	0.71	1.36	(2.2,5.5)	(2.0,4.0)	2.7	0.47	1.05	(2.19,4.3)	(2.0,3.4)	2	0	0.94	(2.0,2.0)	(2.0,2.0)
Heath7	Sept	6	2.4	1.63	(6.0,6.0)	(6.0,14.0)	8.5	2.17	2.36	(6.6,16.9)	(6.0,11.67)	8	1.89	1.83	(6.42,15.6)	(6.0,10.1)	6	2.69	1.63	(6.0,6.0)	(6.0,14.0)
Heath8	July	2	0	----	(2.0,2.0)	(2.0,2.0)	2	0	----	(2.0,2.0)	(2.0,2.0)	2	0	----	(2.0,2.0)	(2.0,2.0)	2	0	0	(2.0,2.0)	(2.0,2.0)
Heath8	Sept	7.8	3.49	2.55	(7.0,30.8)	(7.0,18.67)	10.5	2.66	2.75	(7.9,20.1)	(7.2,13.83)	9.7	1.94	2.11	(7.7,16.6)	(7.67,11.8)	7.8	4.81	2.55	(7.0,40.3)	(7.0,25.64)
Heath9	July	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Heath9	Sept	3	0	----	(3.0,3.0)	(3.0,3.0)	6	2.48	2.45	(3.7,15.4)	(4.0,8.0)	5	1.81	1.86	(3.5,12.1)	(3.68,6.4)	3	0	0	(3.0,3.0)	(3.0,3.0)
Heath10	July	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Heath10	sept	2	0	----	(2.0,2.0)	(2.0,2.0)	4	2.05	2	(2.4,12.6)	(2.0,6.0)	3.4	1.33	1.52	(2.3,8.8)	(2.0,4.1)	2	0	0	(2.0,2.0)	(2.0,2.0)
Meadow1	July	3	0	----	(3.0,3.0)	(3.0,3.0)	6	2.38	2.45	(3.8,14.8)	(4.0,8.0)	5	1.82	1.86	(3.5,12.2)	(3.68,6.4)	3	0	0	(3.0,3.0)	(3.0,3.0)
Meadow1	sept	4	1.47	2.71	(3.1,11.2)	(3.0,5.67)	4.8	1.71	1.96	(3.4,11.7)	(3.0,7.0)	4.3	1.35	1.49	(3.3,9.9)	(3.0,5.7)	4	1.52	2.71	(3.1,11.5)	(3.0,5.67)
Meadow2	July	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Meadow2	sept	6.7	2.79	5.08	(4.5,18.4)	(4.0,12.0)	6.8	2.2	2.42	(4.7,14.9)	(4.5,9.0)	6	1.83	1.83	(4.4,13.2)	(4.67,7.4)	7.2	4.41	6.83	(4.4,28.1)	(4.0,17.0)
Meadow3	July	4	0	----	(4.0,4.0)	(4.0,4.0)	8	2.83	2.83	(5.2,17.9)	(5.0,11.0)	6.7	1.93	2.15	(4.8,13.5)	(5.37,8.1)	4	0	0	(4.0,4.0)	(4.0,4.0)
Meadow3	sept	3.3	2.01	2.79	(2.2,13.3)	(2.0,6.67)	3	1.41	1.41	(2.1,9.8)	(2.0,5.0)	2.7	0.48	1.05	(2.2,4.4)	(2.0,3.4)	3.5	2.34	3.26	(2.2,15.3)	(2.0,7.81)
Meadow4	July	1	0	----	(1.0,1.0)	(1.0,1.0)	1	0	----	(1.0,1.0)	(1.0,1.0)	1	0	----	(1.0,1.0)	(1.0,1.0)	1	0	0	(1.0,1.0)	(1.0,1.0)
Meadow4	sept	5	0	----	(5.0,5.0)	(5.0,5.0)	10	3.21	3.16	(6.6,20.8)	(7.0,13.0)	8.4	2.36	2.4	(6.0,16.6)	(6.37,10.5)	5	0	0	(5.0,5.0)	(5.0,5.0)
Meadow5	July	3	0.42	----	(3.0,3.0)	(3.0,4.0)	3.7	0.78	1.31	(3.1,7.1)	(3.0,6.0)	3.7	0.53	1.05	(3.2,5.7)	(3.0,5.1)	3	0.78	0	(3.0,3.0)	(3.0,4.89)
Meadow5	sept	5	0	----	(5.0,5.0)	(5.0,5.0)	10	3.15	3.16	(6.6,20.5)	(7.0,13.0)	8.4	2.4	2.4	(6.0,16.8)	(6.37,10.5)	5	0	0	(5.0,5.0)	(5.0,5.0)
Meadow6	July	4	1.48	2.71	(3.1,11.3)	(3.0,5.67)	4.8	1.74	1.96	(3.4,11.8)	(3.0,7.0)	4.3	1.4	1.49	(3.3,10.2)	(3.0,5.7)	4	1.65	2.71	(3.1,12.4)	(3.0,5.67)
Meadow6	sept	4	1.5	2.71	(3.1,11.4)	(3.0,5.67)	4.8	1.68	1.96	(3.4,11.5)	(3.0,7.0)	4.3	1.35	1.49	(3.3,9.9)	(3.0,5.7)	4	1.69	2.71	(3.1,12.8)	(3.0,5.67)
Meadow7	July	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Meadow7	sept	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Meadow8	July	4	1.45	2.71	(3.1,11.1)	(3.0,5.67)	4.8	1.6	1.96	(3.4,11.1)	(3.0,7.0)	4.3	1.38	1.49	(3.3,10.1)	(3.0,5.7)	4	1.74	2.71	(3.1,13.1)	(3.0,5.67)
Meadow8	sept	4	0.54	----	(4.0,4.0)	(4.0,6.67)	4.5	0.8	1.26	(4.1,8.5)	(4.0,6.83)	6	1.83	1.83	(4.4,13.2)	(4.67,7.4)	4	1.32	0	(4.0,4.0)	(4.0,10.0)
Meadow9	July	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Meadow9	sept	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Meadow10	July	2	0	0.94	(2.0,2.0)	(2.0,2.0)	2.8	0.71	1.36	(2.2,5.6)	(2.0,4.0)	2.7	0.47	1.05	(2.19,4.3)	(2.0,3.4)	2	0	0.94	(2.0,2.0)	(2.0,2.0)
Meadow10	sept	5	0	---	(5.0,5.0)	(5.0,5.0)	10	3.21	3.16	(6.6,20.8)	(7.0,13.0)	8.4	2.36	2.4	(6.0,16.6)	(6.4,10.5)	5	0	0	(5.0,5.0)	(5.0,5.0)

Appendix 3: Regression models

Table 2 Results from the linear regression analysis, the ":" indicates interaction among two variables, Np=Number of parameters, df=degrees of freedom, Res.SE = Standard error of the residuals, R^2 = coefficient of determination, AIC_c = Akaikes Information Criterium, corrected for small sample sizes.

Model	Np	df	Res. SE	R^2	p-value	AIC_c	ΔAIC_c
$N_{snap\text{-}traps}$~Mh_{JK2} + Habitat + (Mh_{JK2} : Habitat)	4	36	2.41	0.364	0.0008	190.96	0
$N_{snap\text{-}traps}$~Mh_{JK2} + (Habitat) + (Mh_{JK2} : Habitat) + Sex	5	35	2.37	0.404	0.0009	190.958	0.002
$N_{snap\text{-}traps}$~Mh_{JK2} + (Habitat) + (Mh_{JK2} : Habitat) + Age	5	35	2.423	0.377	0.0019	192.754	1.798
$N_{snap\text{-}traps}$~Mh_{JK2} + (Habitat) + (Mh_{JK2} : Habitat) + Period	5	35	2.43	0.374	0.0021	192.957	2.001
$N_{Snap\text{-}traps}$~Mh_{JK2}+Habitat+Age+Sex	5	35	2.45	0.366	0.0026	193.49	2.532
$N_{Snap\text{-}traps}$~Mh_{JK2}+Period+Habitat+Age+Sex	6	34	2.41	0.402	0.0027	193.93	2.973
$N_{Snap\text{-}traps}$~Mh_{JK2}+Habitat+Age	4	36	2.51	0.312	0.0035	194.13	3.178
$N_{Snap\text{-}traps}$~Mh_{JK2}+Period+Habitat+Age	5	35	2.49	0.345	0.0043	194.75	3.791
$N_{Snap\text{-}traps}$~Mh_{JK2}+Habitat	3	37	2.58	0.251	0.0047	195.03	4.069
$N_{Snap\text{-}traps}$~Mh_{JK2}+Habitat+Sex	4	36	2.58	0.273	0.0087	196.30	5.339
$N_{Snap\text{-}traps}$~Mh_{JK2}+Period+Habitat	4	36	2.59	4.456	0.0092	196.44	5.480
$N_{Snap\text{-}traps}$~Mh_{JK2}+Age	3	37	2.66	0.207	0.0138	197.34	6.382
$N_{Snap\text{-}traps}$~Mh_{JK2}	2	38	2.71	0.155	0.0119	197.50	6.547