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Effects of trap density and duration on vole abundance indices

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This study aims to investigate if patterns of immigration by voles into removal plots on the third day of trapping are evident in the grey-sided vole, and if altering the number of traps at each station will result in increased precision of the vole abundance estimate. Traps were placed using the small quadrat method, with one, three, or five traps placed at each corner. Traps were checked twice a day for five days. Mixed-effect models were used to investigate the relationship between the number of traps and the length of time the traps were out on the abundance index. There was no difference between having three or five traps. Having one trap resulted in an inflated estimate. Five traps had the highest number of successful trapping events, reducing the number of zeros in the data set and leaving fewer individuals unaccounted. There was a peak in catches on the third day, driven by younger individuals and by males. These are suspected immigrants that are exploiting the territories left by individuals trapped in the first two days, suggesting this is not a closed system.

Introduction

Understanding population abundance of microtines is important for several reasons. Voles and lemmings are key species in arctic ecosystems and are an important prey species for numerous arctic and subarctic predators, including the arctic fox, which is critically endangered in Fennoscandia. Rodent populations in northern Fennoscandia are typically cyclic (Henttonen *et al*. 1987, Hanski *et al*. 1991, Hansson & Henttonen 1998, Korpimäki *et al*. 2002, Callaghan *et al*. 2004), which has a significant impact on both their food plants and their predators (Ims & Fuglei 2005).

In the subarctic and arctic regions of northern Scandinavia, there have been noticeable declines in three rodent species (*Myodes glareolus, Microtus agrestis* and *Myodes rufocanus*) since the 1970s, which will likely have far-reaching negative effects on their predators, including the arctic fox and the great grey owl among others (Callaghan *et al*. 2004, Christensen *et al*. 2008, Hipkiss *et al*. 2008). Once the dominant species and cyclical in abundance, the grey-sided vole, *Myodes rufocanus*, has become less abundant with irregular population dynamics (Hörnfeldt 2004, Hörnfeldt *et al*. 2006, Ims *et al*. 2008). These declines in both the intensity and regularity of vole cycles in Fennoscandia are not well understood, but they may be caused by a combination of changes in forest management practices and a warmer winter climate, which leads to less stable winters and less protective snow cover (Ecke *et al*. 2002, Christensen *et al*. 2008, Hörnfeldt 2004). Although the cause of these recent changes is not understood, having an understanding of vole population dynamics allows for better management of their predator populations.

For studies to be comparable across different regions and among different species, the methodology itself must be comparable. Several different methods are currently used in rodent monitoring, both with regards to the methodology used in the field, and the ways in which results are presented. In the field, there are two principal methods in achieving this goal, using mark–recapture (live trapping) techniques, or using a removal method (snap-trapping) and constructing abundance indices. Although abundance indices do not use abundance estimates in their calculations, it has been considered sufficient and a number of well-known vole population time series are based on indices rather than density estimates (e.g., Henttonen *et al*. 1985, Hanski *et al*. 1994, Hansen *et al*. 1999, Slade & Blair 2000, Saitoh *et al*. 2006). Abundance indices assume that counts are proportional to (and therefore an index of) population size (Slade & Blair 2000). Despite the time saving effort of using abundance indices, it is far from a perfect method and has been heavily criticized (McKelvey & Pearson 2001). Seasonality may influence the probability of capture (trapability) in some species, and trapability may differ between species, both of which must be taken into consideration when comparing abundance estimates within and among species (Slade & Blair 2000).

Within mark–recapture and removal methods, there are further dichotomies. Live traps may be single capture (Sherman and Longworth) or multi-capture (Ugglan Special). Within index sampling, traps may be placed in a selective or systematic manner. Selective sampling techniques place traps only in areas where voles are likely to be found, however it is easier to create density projection models around the systematic approach. Within systematic index sampling, stations may be organized as either transect lines, or in a large quadrat referred to as the standard minimum technique (e.g. Grodzinski *et al*. 1966, Hansson 1968, Pucek 1969, Viitala 1977, *see*

Table 1. Summary of the field methods used to perform rodent population analyses broken down by the source publication, the number of times this publication was cited by others in peer-reviewed journals (obtained from the *Web of Science*), use of live or snap traps and the spatial configuration of traps, the method by which the raw data was presented, number of traps and stations used, distance between stations, duration of trapping, total area covered by trapping and bait used. Variability in the entries reflects differences in sampling methods within the study, and blank spaces indicate an missing information in a publication.

Source	Cited	Method		Results presented	Traps/ station	No. of stations	Distance between stations (m)	Days out	Size (m, unless other unit is given)	Bait
Stickel 1948	28	Live	Sherman, quadrat	Count	1	177	15	6	3.4 ha	Oats and peanut butter
Stickel 1948	28	Live	Sherman, transect	Count	1	40	4.6	4	182.9	Oats and peanut butter
Andrzejewski *et al.* 1966		Live		Count	1–7	60–140	15		1–2.3	Oats
Grodzinski *et al.* 1966		Snap trap	Standard minimum	Cumulative % of catch	2	256	15	7	225 × 225	Apple
Krebs 1966	2	Live	Longworth quadrat	Count; Density	1–2	75–210	9 × 4.6	2–3	0.33-0.8ha	Oats

Ryszkowski *et al.* 1966		Live		Population estimate (Mark recapture)	2	256	15	21	225 × 225	Oats
Hansson 1968	23	Snap trap	Line transect	Density; Relative catch	2	25	25	5	125	Unbaited
Pucek 1969		Snap trap	Standard Minimum	Index of trappability	2	256	15	7	225 × 225	Apple
Yang *et al.* 1970	10	Live	Longworth quadrat	Population estimate Voles/100 trap nights	1	100	7.6	2	68.5 × 68.5	Oats
Myllymäki 1971b		Snap-trap	Small quadrat	Count	3	4	15	4	30–44 SQ	Apple
Wallin 1971	2	Live	Two multi, one single (quadrat)	Frequency distribution of trap captures	3	40	> 25	3	500 × 700	
Barbehenn 1974		Snap trap	Standard minimum	Count, Catch/no. of traps; Catch/ 2 day period	1	64	15			Polish wicks
Myllymäki 1977	169	Live	Sherman, quadrat	Catch Index; Count;	2	4	5–10	1	4 × 4	Oats
Viitala 1977	151	Snap trap	Line transect	Trappability	2	25	7	1	350	Bread, apple
Löfgren 1995	22	Live	Ugglan special	Density	1	196–256	15	6	14 × 14–16 × 16 rows	
Ishibashi *et al.* 1998	18	Live	Sherman, quadrat	Count	2	300	10	3	200 × 150	Apple
Yoccoz *et al.* 1998	38	Live	Sherman, quadrat	Population size/ demography (mark-Recapture)	1	100	10	3	100 × 100	Oats
Hansen *et al.* 1999	60	Snap trap	Line transect	Voles/100 trap nights	2	40–70	7	2	300–500	Bread
Hansson 1999	57	Snap trap	Small quadrat	Mean catch/SQ; count	3	4	15	4	10–30 SQ	Apple
Johannesen and Mauritzen 1999	9	Live	Ugglan special	Density	1	84–156	15	3	1.4 ha	Oats, carrot, apple
Morris *et al.* 2000	33	Live	Longworth, quadrat	Count	1	25	15	3	60 × 60	Oats and apple
Blackwell *et al.* 2002	8	Snap trap	Line transect	Voles/100 trap nights; Density; count	1	13	25	5	325	Peanut butter
Ecke *et al.* 2002	30	Snap trap	Line transect	Count	3	15	30	3	420	Polish wicks
Christensen & Hörnfeldt 2003	10	Snap trap	Line transect	Voles/100 trap nights	4	10	10	3	100	
Krebs *et al.* 2003	16	Snap trap	Line transect	Density	3	20	15	3	300	Peanut
Hopkins & Kennedy 2004	7	Live	Sherman, transect	Count; Catch per Unit Effort	1	10	15	3	150	Oats
Hopkins & Kennedy 2004	7	Live	Sherman, quadrat	Count; Catch per Unit Effort	1	150	15	14	225 × 225	Oats
Boonstra and Krebs 2006	11	Live	Longworth, quadrat	Density	1	50	20	1.5	2.81 ha	Oats

Table 1). In both instances, trap stations are assigned at regular intervals along a transect or grid, regardless of the local habitat (Table 1). Alternatively, there is the small quadrat method, which includes aspects of both systematic and selective sampling. It is systematic in nature in that traps are placed in a small quadrat with a uniform distance between each station, and a uniform number of traps at each station (Myllymäki *et al*. 1971a, 1971b). However, since each quadrat is placed separately in a definable habitat, the problem of placing traps where voles are not likely to occur is avoided (Myllymäki *et al*. 1971b). Additionally, the small quadrat method and the placing of multiple traps at a single location avoids the problem of trap saturation (Henttonen *et al*. 1987, Xia & Boonstra 1992, Hanski *et al*. 1994). For these reasons, small quadrats may produce more reliable density estimates than live catches (Myllymäki *et al*. 1971b). Inconsistencies still exist among all these different techniques, primarily regarding the number of traps per station, the number of days traps are left out, and the bait used (Table 1). These differences may lead to violations of assumptions when using abundance indices.

Previous Finnish studies have taken this issue into consideration by testing the effect of the number of days traps were left out on the field vole abundance estimate (Myllymäki *et al*. 1971a, 1971b). These studies found evidence of a “third-day syndrome” where the estimate is inflated on the third day of trapping due to immigration (Myllymäki *et al*. 1971b). This study aims to build upon this earlier work by investigating the effect of the duration of trap sampling and the number of traps at each station on the abundance estimate of the grey-sided vole.

Material and methods

Study site

Sampling took place in the last two weeks of July 2007 in the Ritsem regions of northern Sweden (Ritsem, 67°40´N, 17°40´E). This was considered to be a “moderate-high” year for vole populations, and it was found later to be the summer directly preceding a “peak” year, which occurred the following spring. The average annual temperature for July is 10.7 °C, with an average precipitation of 63 mm (Swedish Meteorological and Hydrological Institute, www.smhi.se). Our sampling year had slightly higher than normal temperatures (July average temperature 11.3 °C), and slightly above-average precipitation (67.1 mm; www.smhi.se). Sampling elevation varied between 418 m above sea level and 592 m a.s.l., with the treeline located at approximately 700 m a.s.l.

Sampling occurred in relatively homogenous habitats where the dominant understory vegetation was grass, *Carex* spp., European blueberry or bilberry (*Vaccinium myrtillus*), *Empetrum nigrum*, *Juniperus communis*, *Salix* spp., dwarf birch (*Betula nana*), and members of the Ericacacea family (e.g, *Vaccinium* spp.). Dominant herbivores in the regions vary, but three species of voles, (*Microtus agrestis*, *Microtus oeconomus*, *Myodes rutilus*) were present in most areas. The study site is part of an ongoing rodent monitoring program, and has been used for approximately ten years.

Species

Myodes rufocanus (syn. to *Clethrionomys rufocanus*) is characterized and easily identifiable by a red back and grey side, more commonly referred to as the grey-sided vole. It was used as our study species due to its dominance in abundance at the study site. Palearctic in distribution, the grey-sided vole ranges from Japan through Siberia and has a western extent of Scandinavia (Kaneko *et al*. 1998). It is typically cyclic in abundance and cycles have become increasingly variable in recent years (Kaneko *et al*. 1998). Litter sizes vary between four and seven individuals and maturity is usually reached after 30–60 days, varying on population density, social factors and season (Kaneko *et al*. 1998). The grey-sided vole typically favours forests, but may often be observed in open habitats as well (Kaneko *et al*. 1998). Its main food type, the deciduous dwarf shrub bilberry (European blueberry), is especially important during winter when it is the dominant food source (Laine & Henttonen 1987, Hansson & Henttonen 1998).

Old growth pine forest may be important for the occurrence of grey-sided voles in some areas (Ecke *et al*. 2006, Christensen *et al*. 2008).

Study design

In eight different locations using snap-traps, six small quadrats were clustered together in close proximity with a distance of at least 70 m between each small quadrat and 15 m between each station within each small quadrat (Fig. 1). The larger clusters of small quadrats were run in simultaneous sets of three, except for the last set which had two. Habitat was homogenous within each large quadrat. Small quadrats were divided evenly to have one, three or five traps per station. We used one, three, and five traps per station in our design since we were investigating the effects of trap saturation on vole abundance indices. Traps were baited with peanut butter and raisins and checked twice a day for five days. Animals caught were identified, sexed, and aged using maturity as an indicator (juvenile, subadult and adult categories). The stage of maturation was determined on a combination of characteristics and dissections where presence/absence of foetuses and placental scars were noted. The total sampling effort was 2880 trap nights and yielded a total of 175 grey-sided voles.

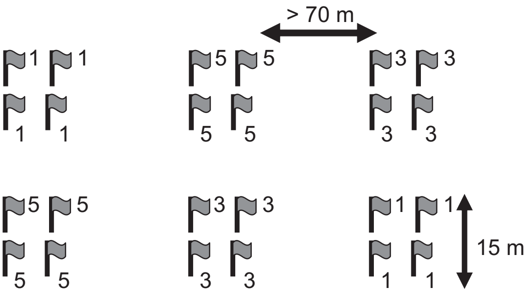

Fig. 1. Diagram depicting the snap-trap layout. At each trap station within each small quadrat there were either one, three or five traps per station, and each station was 15 m apart. Small quadrats were clustered together in groups of six to form one large quadrat, and were placed in a habitat where it seemed likely grey-sided voles would be located. The minimum distance between each small quadrat in this cluster was 70 m.

Analysis

All analyses were conducted in the open sourced statistical package, R (ver. 2.6.1, R Development Core Team 2007). The cumulative number of snap-trap events per quadrat was converted to a proportion of successful trapping events (full trap) over the number of unsuccessful trapping events (empty trap), hereafter referred to as the catch/no-catch ratio, after each day of trapping (pooled days are evening and morning, encompassing the overnight period) for the five-day trapping period in each of the small quadrats.

Due to the complex nature of our experimental design where six small quadrats were clustered together to form one large quadrat, samples within each large cluster were more likely to resemble each other than they were to samples in another quadrat, which may have naturally different vole densities. If these data were to be inappropriately modelled, the residuals within the samples would be correlated rather than being independent of each other. To take this lack of independence into consideration we used mixed-effect models to incorporate the random effects within the experimental design so that correlations and homogeneity of the residuals can be avoided. Mixed-effect models allow for the spatial autocorrelation of our dataset to be explicitly incorporated into the model analysis (Pinheiro & Bates 2000, Zuur *et al*. 2009). The mixed effect models were hierarchical in design, meaning that we started with the most complicated model including all of the interaction effects, and insignificant terms were removed one at a time. Models were compared using Akaike's information criterion (AIC; Burnham & Anderson 2002). Mixed effect models were constructed using the lme4 package in R. Other libraries used in this analysis include the lme, grid, lattic, bblme and multcomp packages. All results were considered significant at $p < 0.05$.

While constructing the generalized linear mixed model for the number of traps per station and the number of days traps were left out, the dependent variable was measured by combining the number of successful and unsuccessful trapping events, thus having a binomial error structure. Day and number of traps were treated as fixed effects while site and quadrat (SQ) were

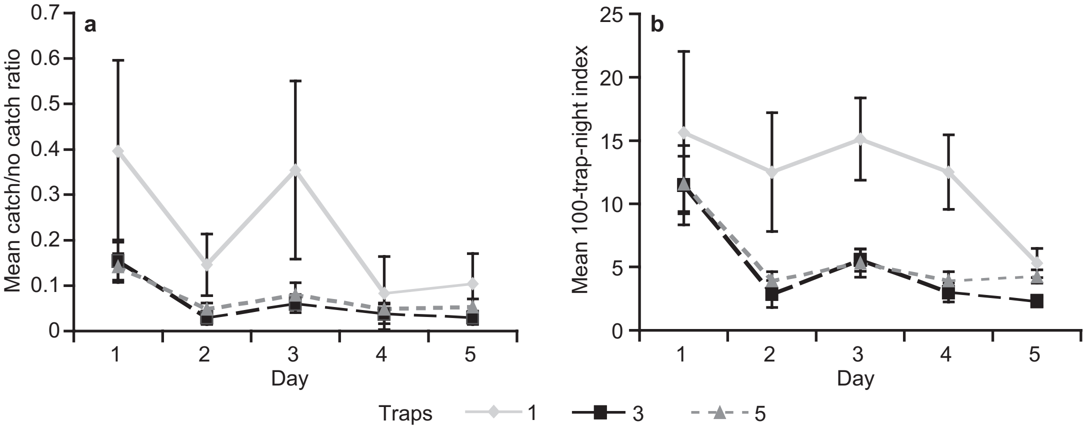

Fig. 2. Grey-sided vole abundance estimates using (**a**) the mean number of voles caught as a function of the number of traps full/number of traps empty and (**b**) the mean 100 trap night index. Both estimations are shown over the course of five days with one, three or five traps per station, ± SE (*n* = 16 for either one, three, or five traps/station for each day 1–5).

treated as random effects. A generalized linear model using Poisson error structure was used to determine if there was a difference in number of successful trapping events in each quadrat due to the number of traps.

After initial analysis, we noticed a small peak in trapping events that occurred on the third day of sampling, and we further analyzed the data to see if trapping events were correlated with a specific age or sex class. The generalized linear mixed model for the age and sex of the individual caught was analysed with a Poisson error structure and catches from all small quadrats within a large quadrat were combined. A generalized linear model analysis was performed on the count data. The initial model could not include the three-way interaction (sex × age × day) since no juvenile females were caught in the first three days of trapping, so comparing any juveniles against the intercept would result in error.

Table 2. Generalized Linear Mixed Model summary of results for catch/no-catch ratio as a function of the number of traps per station and the number of days left out.

Parameter	Estimate	SE	*z*	*p*
Intercept	–1.638	0.390	–4.203	< 0.001
3 Traps	–0.755	0.321	–2.348	0.019
5 Traps	–0.485	0.300	–1.614	0.106
Day 2	–1.151	0.246	–4.681	< 0.001
Day 3	–0.635	0.213	–2.991	0.003
Day 4	–1.561	0.282	–5.531	< 0.001
Day 5	–1.195	0.249	–4.793	< 0.001

Results

There were no significant interaction effects, but there were significant differences in the catch/no-catch ratio depending on both the number of traps left at each station and the number of days that the traps were left out (Table 2).

The catch/no-catch ratio was significantly highest when the quadrat had only one trap per station, and was significantly highest the first day of trapping (Fig. 2 and Table 2; *n* = 16). The catch/no-catch ratios were similar for quadrats with both three and five traps per station, and were generally much lower than the ratio for only one trap per station, although not significantly different from each other (Fig. 2; *n* = 16). They both followed the same general trend over time where the ratio was significantly highest on the first day of trapping, then fell on the second day, followed by a small but significant peak on the third day, which led to a difference between having the traps out either two or three days and four days (Fig. 2 and Table 2; *n* = 16).

Having a quadrat with five traps per station resulted in significantly more successful trapping events than having only one or three traps per station (Fig. 3, $n = 16$; one trap: estimate = –0.916, SE = 0.177, $z = -5.183$, $p < 0.001$; three traps: estimate = 0.341, SE = 0.231, $z = 1.474$, $p = 0.140$; five traps: estimate = 1.088, SE = 0.204, $z = 5.324$, $p < 0.001$). There was no significant difference between having one or three traps per station (estimate = 0341, SE = 0.231, $z = 1.474$, $p = 0.140$).

When analyzing the data taking age/sex into consideration, the model was reduced to include only up to the two-way factors of sex × day and age × day, at which point all the factors were significant so the model was not reduced any further. There were significant two-way interactions for both sex × day and age × day, as well as day and age both being significant on their own. A multiple comparison of means test found that both juveniles and sub-adults were significantly different from adults, but not from each other.

On day one, most catches were adults, followed by sub-adults, then by juveniles (both sexes), and there were more females caught than males (Fig. 4 and Table 3). This trend continued on day two, this time with more males being caught than females (Fig. 4). On day three there was a shift where fewer adults were caught and instead more sub-adults and juveniles were caught (Fig. 4 and Table 3). This was especially the case for males. The number of voles caught continued to decline on day four, with a more even distribution between the age and sex classes. This trend then continued for day five (Fig. 4).

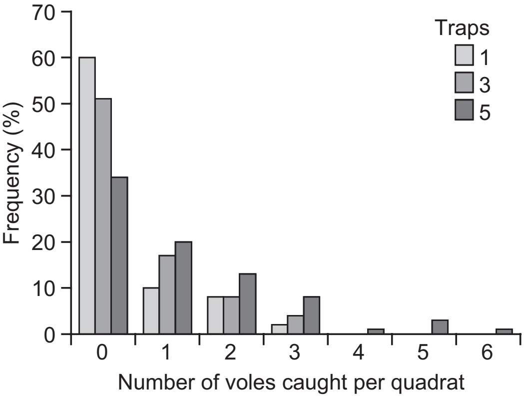

Fig. 3. Number of trapping events per quadrat with either one, three or five traps per station, combined daily total for all five days (maximum possible number of voles trapped per quadrat is four, 12 and 20 for one, three and five traps per station, respectively, $n = 16$).

Discussion

The number of traps per station had a significant effect on the catch/no-catch ratio. Quadrats with only one trap per station consistently had a higher catch ratio than those with three or five traps per station. This was likely due to trap saturation. In areas of moderate vole density when there was only one trap per station, all traps in the quadrat were full. When this estimate of 100% full traps is extrapolated to a larger area, the vole density is overestimated. However, if there is only one trap per station in a low-density area, it is prob-

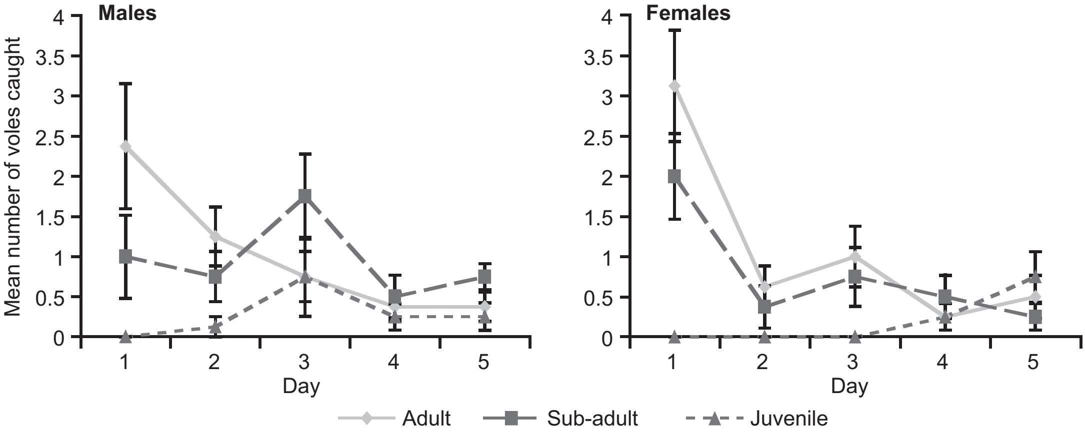

Fig. 4. Mean ± SE ($n = 8$) number of voles caught each day, per age-class (adult, sub-adult and juvenile) and sex (males and females).

able that all (one) trap(s) are empty, resulting in a zero catch/no-catch ratio, which may not be the case when there are more traps per station since they can exploit more probable trap locations (holes, under shrubs, etc.). This also amplifies the effects of intersite variation, which results in high variance in the data, a very high standard error and low precision.

There was no difference in the catch/no-catch ratio for quadrats with either three or five traps per station, meaning that the higher trapping effort required for five traps per station does not result in a more accurate estimate of the vole population. This is because even at moderate to high-density vole locations, there was usually at least one trap open at each station for both three and five traps per stations, and there was still an opportunity to catch another animal. Since vole densities were never high enough that five traps per station were saturated, three traps per station seem to give adequate results. However, five traps per station also resulted in significantly fewer stations having zero trapping events, suggesting that when there are only one or three traps per station there are significantly fewer sites where grey-sided voles exist but are not observed (Fig. 2). This is important to take into consideration if the goal of the study is to examine the species richness of an area by analyzing presence/absence data in a particular habitat patch. While increasing the number of traps may lead to a deflated index ("trap-unsaturation"), this occurs on a larger spatial scale than trap saturation and was not the focus of our study. Adding two extra traps per station from the current norm of three traps per station increases numerical effort, but in practical terms it does not require any more human effort to simply set out more traps when laying trap lines. For this reason, having five traps per station should be considered since it increases the precision and reduces variation of the vole abundance estimate.

Table 3. Generalized Linear Mixed Model summary of results for differences in the age and sex of voles caught for each day.

Parameter	Estimate	SE	*z*	*p*
Intercept	1.184	0.181	6.556	< 0.001
Males	–0.381	0.245	–1.556	0.120
Juveniles	–3.784	1.011	–3.742	< 0.001
Sub-adults	–0.606	0.254	–2.389	0.017
Day 2	–1.695	0.429	–3.948	< 0.001
Day 3	–1.674	0.388	–4.316	< 0.001
Day 4	–2.408	0.547	–4.405	< 0.001
Day 5	–1.968	0.464	–4.242	< 0.001
Males				
Day 2	1.135	0.494	2.298	0.022
Day 3	1.000	0.412	2.426	0.015
Day 4	0.499	0.544	0.917	0.359
Day 5	0.294	0.484	0.608	0.543
Juveniles				
Day 2	1.076	1.445	0.744	0.457
Day 3	2.937	1.123	2.616	0.009
Day 4	3.561	1.214	2.934	0.003
Day 5	3.918	1.136	3.449	< 0.001
Sub-adults				
Day 2	0.095	0.492	0.194	0.846
Day 3	0.963	0.431	2.234	0.026
Day 4	1.076	0.624	1.725	0.084
Day 5	0.740	0.576	1.283	0.199

Results also show that the traps should be left out at the very least for two days. There was a significant difference in the catch/no-catch ratio between day one and day two. Ideally, traps should be left out until there is a drop in the number of successful trapping events. Our data showed a small peak on the third day of trapping. This "third-day syndrome" appears to be caused by an influx of sub-adults and juveniles seeking territories and exploiting those left by dominant male voles caught during the first two days of trapping. Territoriality is an important part of vole dynamics, usually influencing populations through direct density dependence (Ishibashi *et al.* 1998). Females typically defend territories for the purpose of breeding, while the territories of males generally encompass the territory of several females (Ishibashi *et al.* 1998). Males are more likely to disperse and tend to disperse over larger areas than females (Ims, 1989, Ishibashi *et al.* 1998). Additionally, males are more likely to have mutually exclusive home ranges, as compared with females, which would lead to older males being dominant, while younger males may be more transient while searching for a territory (Ims 1989).

Previous Finnish studies found evidence of this "third-day syndrome" (Myllimäki *et al.* 1971b). When traps are out for five days, 40%–50% of (male) juveniles were caught on day three, not in the first two days like with other demographics (Myllymäki *et al.* 1971b). This is suspected to be because of the high edge effect (and correspondingly, the proportion of invaders) associated with smaller quadrats or transect lines (Myllymäki *et al*. 1971a, 1971b). This means that after three days of sampling, the proportion of outsiders in the catch is high (Myllymäki *et al*. 1971a, 1971b). Male voles will typically notice the disappearance of a neighbor and will investigate a vacated area, which also helps to explain an increased rate of invasive sub-adult males (Myllymäki *et al*. 1971a). The removal of the older, dominant males in the first few days spurs the immigration of sub-adult/juvenile males into the vacated territory and results in an increase in sub-adult/juvenile males on the third day of trapping (Myllymäki *et al*. 1971a). We then suspect that after the first few days of trapping the older dominant males are caught and their home ranges are vacant, soon to be filled by younger males. Although the three-way effect (age × sex × day) was unable to be included into the model for this study, we propose that if we had designed the study to look for immigrants on day three, we would have found that they were primarily juveniles and sub-adult males. Given the evidence of this "third-day syndrome", leaving the traps out for three days or more may lead to erroneous results by over-estimating population size and the carrying capacity of the area due to immigration into the quadrat. Dispersal is known to be more prominent at exceptionally low and high population densities (Ishibashi *et al*. 1998, Ims & Andreassen 2005). Our study was performed during a year of moderate/high vole density, which may explain why this trend was not previously observed at our study site. Regardless, this indicates that the study site is not a closed system when trapped for more than two days, as previously assumed by other studies and their population estimate models (e.g. Otis *et al*. 1978).

An important part of arctic ecosystem management is having a good understanding of small mammal populations in the circumpolar area, which means that methodology used must be comparable throughout the circumpolar community. The final conclusion of this study is that when attempting to study vole abundance, five traps per station should be left out for two days. If trapping occurs for more than two days, statistical analysis must take immigration (non-closure) into consideration. It is important to note that this paper does not resolve the question of identifying the most efficient removal method for estimating vole population densities. Rather, it highlights some of the problems with current methodological designs, and will hopefully encourage further investigation into this issue. Given the differences in our results and what was previously known at our study site, further studies should be conducted concerning the differences in trapability for different vole species at different periods in their population cycle.

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