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Quantifying the abundance of small mustelids is important both for conservation purposes and for our understanding of ecosystem processes. Footprint tunnel tracking is one of the techniques now used to index the relative abundance of small mammals; however, there have been few or no previous attempts to calibrate indices of mustelid abundance derived from footprint tunnel tracking. Weasel *Mustela nivalis* abundance was assessed by footprint tunnel tracking and simultaneous live-trapping, either capture-mark-recapture or removal, in six sites in northern England from April 1998 to February 2000. The number of tunnels with weasel footprints was tightly related to the number of weasels live-trapped, although, as expected, the relationship varied with field vole *Microtus agrestis* density and season. Temperature had only a weak effect in the calibration. The same number of tunnels with weasel footprints was equivalent to greater weasel abundance at high vole density than at low vole density. Similarly, weasel abundance was greater for the same number of tunnels with weasel footprints in summer and autumn than in winter and spring. In conclusion, it is important to correct for variation in vole density when using activity indices such as footprint tunnel tracking to sample weasel abundance, otherwise spurious patterns may emerge from the use of such index data.

Key words: density, footprint tracking indices, live trapping, Mustela nivalis, northern England, population cycles, specialist predators, weasel

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The ability to accurately assess the abundance of small mustelids is an essential step in attempting to discern the nature and role of the numerical response of a specialist predator in population cycles of microtine rodents (Hanski & Korpimäki 1995, Korpimäki & Krebs 1996, Turchin & Hanski 1997, May 1999). Conservationists, primarily in New Zealand, also require methods to measure mustelid abundance in order to facilitate the control of populations of introduced stoats *Mustela erminea* and weasels *M. nivalis* (e.g. Murphy, Clapperton, Bradfield & Speed 1998). Relatively few studies have attempted to assess either the absolute abundance or changes in the abundance of weasels or stoats (Lockie 1966, Erlinge 1974, 1977, 1983, King 1975a, Simms

1979, Debrot & Mermod 1983, Delattre 1983, Erlinge & Sandell 1988, Jedrzejewski, Jedrzejewska & Szymura 1995, Alterio, Moller & Brown 1999). Live-trapping studies of such species need to be very intensive to prove useful and are complicated by the low densities at which stoats and weasels typically exist and with the unequal trappability of individuals (King 1975b). While individual capture heterogeneity is not a problem *per se* as the sophisticated capture-mark-recapture methods now in use can account for such biases (Otis, Burnham, White & Anderson 1978), the principal problem is that for weasels and stoats, densities and hence the number of capture histories available, are rarely sufficient to usefully apply such methods. An alternative is to combine data from different methods in order to more accurately estimate the density. However, this requires a huge investment in terms of time, manpower, energy and expenditure (e.g. Jedrzejewski et al. 1995).

Most studies of small mustelids have relied extensively on less intensive surveying techniques, in particular snow-tracking (Fitzgerald 1977, Henttonen, Oksanen, Jortikka & Haukisalmi 1987, Korpimäki, Norrdahl & Rinta-Jaskari 1991, Oksanen & Oksanen 1992, Oksanen & Henttonen 1996) and kill-trapping (Tapper 1979, King 1980, King, Innes, Flux, Kimberley, Leathwick & Williams 1996, McDonald & Harris 1999, Johnson, Swanson & Eger 2000). However, both of these methods have severe limitations. Snow-tracking is necessarily restricted to censusing small mustelid numbers during the winter and is therefore unsuitable for discerning changes in the size of the breeding population and, by definition, kill-trapping has a profound impact on the population under study. In addition, kill-trapping is frequently undertaken primarily to harvest furs or as a means of predator control rather than with any scientific design in mind: sampling is usually directed to areas with the highest abundance and is consequently intrinsically biased. Conclusions drawn from the use of such techniques can therefore be misleading where due care is not taken to account for variation in tracking and trapping rates with, for example, varying prey density, season, snow depth (Jedrzejewski et al. 1995) and survey effort (McDonald & Harris 1999).

Footprint tunnel tracking is an alternative technique used to index the relative abundance of small mammals now in common use in New Zealand, although not elsewhere (King & Edgar 1977, Innes, Warburton, Williams, Speed & Bradfield 1995, Brown, Moller, Innes & Alterio 1996, Murphy et al. 1998, Clapperton, McLennan & Woolhouse 1999). Brown et al. (1996) calibrated tunnel tracking rates of ship rats *Rattus rattus* with estimates of absolute density from removal trapping but found that the number of tunnels used by mice *Mus musculus* increased significantly as the rat and mouse populations were removal trapped. Indeed, Ruscoe, Goldsmith & Choquenot (2001) showed that tracking tunnel indices for mice bore no relationship to estimated mouse population size in a New Zealand beech forest. To date, however, there have been no attempts to formally evaluate and calibrate mustelid footprint tunnel tracking indices (Alterio et al. 1999).

Footprint tunnel tracking has clear advantages over snow-tracking and kill-trapping as it can be used throughout the whole year, including the breeding season, is not destructive and is less likely to be subject to sampling heterogeneity. However, as footprint tunnel tracking indices are actually a measure of small mustelid activity, they are likely to vary with a number of factors, such as prey density and season, in addition to weasel and stoat abundance. Here, I combine information from live-trapping, both capture-mark-recapture and removal, and footprint tunnel tracking of weasels with live-trapping of field voles *Microtus agrestis* in order to take the first steps towards calibrating weasel footprint indices.

Material and methods

The study was carried out in six grass-dominated clear-cut sites, each covering 5-12 ha, in Kielder Forest, northern England (55°13'N, 2°33'W). Kielder is a large man-made spruce forest, managed for commercial timber production. Much of the forest lacks grass cover and is consequently unsuitable habitat for field voles (Petty 1992), however, some 16-17% of the total area is occupied by clear-cuts, dominated by *Deschampsia caespitosa* and *Juncus effusus*. Field vole populations fluctuate cyclically in these grassy clear-cuts with a three to four-year period (mean vole density; range: 25-215 voles ha^{-1}). For a detailed description of the study area see Lambin, Petty & MacKinnon (2000).

Footprint tunnel tracking was carried out at five of the six sites from April 1998 to February 2000, and at the sixth from July 1998 to February 2000 excluding November 1998, following the method described by King & Edgar (1977; Table 1). Sections of plastic drainpipe (50 cm long × 10 cm diameter) were used as tunnels. Each tunnel contained a wooden tracking board with a central well, lined with plumber's cloth, for the chemical 'ink': a mixture of 240 g ferric nitrate, 360 g polyethylene glycol (PEG 300/400) and 810 g water. On either side of the well, on each tracking board, two tracking papers measuring 19 × 7 cm were held in

Table 1. Comparison of weasel trapping and footprint tracking methodology between the six control and removal sites in Kielder Forest.

	Removal Sites			Control Sites		
	1	3*	5*	2	4*	6
Study period	April 1998 - February 2000			April - October 1999		
Type of trapping	Removal			Capture-mark-recapture		
Trapping intensity						
Average	6.5 ± 0.5 nights/month			3.9 ± 0.1 days/month		
Range	3-19 nights/month			3-4 days/month		
Definition of Trap Index	No of weasels caught in 14-day period after tracking tunnels were set			No of weasels caught/month (new captures & primary recaptures)		
Tracking intensity	2 weeks/month during April-October; 1 week/month during November-March†			2 weeks/month during April-October†		
Definition of Print Index	Score for each week			Mean score for each month		
Calibration Sample Size ‡	34	31	33	7	6	7

* No trapping occurred in Site 3 during April, July and October 1998, in Site 4 during October 1999, and in Site 5 during April 1998.

† In Sites 2 and 6 tunnels were operated continuously during July-September 1999, and in Site 5 for 1 week only in April 1998.

‡ Removal sites: excludes tracking weeks where no trapping took place during the defined 14-day period; trapping effort was zero for a total of three, six and three tracking weeks in Sites 1, 3 and 5, respectively.

place using elastic bands. Tracking papers were cut from sheets of brown wrapping paper that had been sprayed, on the rough side, with a solution of 50 g tannic acid in 475 ml ethanol and 475 ml water, and subsequently left to dry.

At each site, 50 tracking tunnels were distributed in a grid at 35 m intervals and operated for two consecutive weeks per month from April to October, and one week per month from November to March; tracking papers were left *in situ* for one week at a time. At two of the control sites (sites 2 and 6), the tracking tunnels were operated continuously from the beginning of July until the end of September 1999 (see Table 1). Tracking tunnels remained in position throughout the study period. The two tracking papers in each tunnel were taken as a single sampling unit and scored for presence or absence of weasel tracks. The Print Index (PI) was calculated as the number of tunnels in which weasel footprints were recorded in any given week, i.e. the weekly tracking rate per 50 tunnels.

At three sites, weasels were live-trapped and removed from April 1998 to February 2000, as part of another experiment (Graham 2001; see Table 1). Twenty-five wooden box traps, built to the design specifications of King (1973), were evenly spaced at each site. Traps were set for an average of 6.5 ± 0.5 nights per month. Traps were baited with previously frozen fish and checked at 24-hour intervals (the use of live bait is ethically questionable and illegal in Britain). All weasels were handled and ear-tagged under anaesthesia using the method described by D.W. Macdonald, M.R. Pullen, T.E. Tew & I.A. Todd (unpubl. manuscript), translocated from Kielder and released in similar habitat a minimum of 10 km from the initial capture site. For each capture, location, identity, sex and weight were recorded. At the other three sites, weasels were live-trapped at monthly intervals from April to October 1999 (one site was not trapped in October 1999; see Table 1). Fifteen traps were operated per site. Traps were set between 06:00 and 08:00 and then checked twice at 6-hour intervals, for an average of 3.9 ± 0.1 days per month. Traps were not set overnight. Individual weasels were marked using PIT tags, in addition to ear-tags; weight was recorded at the initial capture only.

The Trap Index (TI) was calculated as the number of weasels caught per trap day, after allowing for sprung traps including the by-catch of non-target species (Nelson & Clark 1973). To standardise for the different trapping regimes in control and removal sites, 24 hours was considered to be a trapping interval (I) of length 1, therefore the total number of trap days for control sites was multiplied by 0.5 as traps were only set for 12 hours each day. However, as weasels are more active during the day than at night (King 1975a, Jedrzejewski, Jedrzejewska, Zub & Nowakowski 2000; Macdonald et al., unpubl. manuscript), it may be more appropriate to use a value of I between 0.5 and 1: where appropriate, the effect of using I = 2/3 was investigated. For control sites, the total number of new captures and primary recaptures in a given month was used to calculate the Trap Index for each month. Primary recapture was defined as the first capture of an individual, marked in a previous month, in a subsequent monthly trapping session (any further recaptures of the same individual within the monthly trapping sessions were termed secondary recaptures). As the timing and duration of trapping was more frequent but irregular in removal sites, the Trap Index was calculated as the number of weasels caught and the trapping effort in each 14-day period after tracking tunnels were set with papers.

Field vole abundance was estimated every month from March to October 1998 and 1999, and during March 2000, in all six sites. Each site had a permanent live-trapping grid consisting of 100 Ugglan Special

Mouse traps set at 5-m intervals and baited with wheat and carrots. The effective trapping area (0.3 ha) was calculated by adding one trap interval to the outer perimeter of the grid. Traps were pre-baited 2-3 days before each live-trapping session, set at approximately 18:00 and then checked five times at roughly 12-hour intervals, viz. at dawn and dusk (except at two sites in April 1998 when trapping was aborted after only three checks due to adverse weather conditions). Population size was estimated using program CAPTURE (Otis et al. 1978), assuming that no mortality or recruitment occurred during the five secondary sessions. Of the selected models, 71% assumed heterogeneity in the capture probabilities of individuals and differences in the trapping probability between sessions. Vole abundance was, therefore, calculated using the estimator of Chao & Lee (1991). When there were only three secondary sessions the jackknife estimator was used (Otis et al. 1978, Boulanger & Krebs 1996). Values of vole abundance for November-February 1998 and 1999 were interpolated from October and March abundance estimates. Population estimates were divided by the effective trapping area to estimate vole density.

Statistical analysis

Generalised linear mixed models (GLMMs) were used for all analyses of the relationship between the Trap Index and the Print Index, as the Trap Index was count data with non-normal errors. GLMMs were implemented using the GLIMMIX macro in SAS (Littell, Milliken, Stroup & Wolfinger 1996) with a Poisson error distribution and logarithmic link function: data were corrected for over- or underdispersion. As Trap Index values were non-integer, the actual number of weasels trapped was used as the response variable in the GLMMs with the trapping effort as an offset: therefore the values predicted by the model were the number of weasels caught per trap day. To control for any variation between sites, site was included in models as a random factor. Models were selected using SAS type III tests (SAS 1990) by fitting the most saturated model first and subsequently eliminating the least significant terms one at a time, in a stepwise backward procedure until all terms in the model had probability values less than or equal to 0.01. Denominator degrees of freedom were calculated, in SAS, using Satterthwaite's formula (Littel et al. 1996). Unless stated otherwise, analyses were carried out separately for control and removal sites.

To obtain the best fitting calibration between the Trap Index and the Print Index, the relationship was modelled using GLMMs, with season (two levels) and vole density (continuous variable) as covariates in the model. Months were grouped into two seasons: winter/spring (December-May) and summer/autumn (June-November). I also investigated the effects of site type (two levels: control, sites 2, 4 and 6; and removal, sites 1, 3 and 5), year (two levels: year 1, March 1998 - February 1999; and year 2, March 1999 - February 2000) and temperature (mean minimum temperature in °C, at grass level at 09:00 at Kielder Castle for the tracking session). To conserve the observed linear relationship between the Trap Index and the Print Index in the model, Print Index scores were first transformed by taking ln (PI + 1).

Results

Print Index (PI) scores ranged from 0 to 21 (per 50 tunnels). Log-transformed Print Index scores (ln (PI + 1)) in the second week of each month were linearly related to those in the first week (control sites: week 2 = 0.83(0.10)*week 1 + 0.27(0.14); $R^2 = 0.61$, $N = 42$, $P < 0.001$; removal sites: week 2 = 0.59(0.12)*week 1 + 0.45(0.15); $R^2 = 0.36$, $N = 44$, $P < 0.001$). Values in brackets are the standard errors of parameter estimates. If the number of weasels in each site was constant between weeks in the same month, the slopes of both relationships should have been close to 1. However, the regression coefficient for removal sites was signifi-

Table 2. Summary of weasel live-trapping data at the six sites in Kielder Forest during April 1998 - April 2000. Differences in trapping methodology between control and removal sites are outlined in Table 1.

	Removal Sites				Control Sites			
	1	3	5	Total	2	4	6	Total
Total no of trap 'days'*	3720	2820	3760	10300	227 (302)	199 (265)	227 (302)	653 (869)
No. individual weasels trapped								
♂	13	10	28	51	6	1	2	9
♀	8	4	6	18	2	1	0	3
Total	21	15	34	70	8	2	2	12
Total no of captures	21	15	34	70	19	2	17	38
Capture rate*†	0.6	0.5	0.9	0.7	6.2(4.6)	1.0 (0.8)	3.5 (2.6)	3.7 (2.8)

* Values in parentheses were calculated using trapping interval I = 2/3, otherwise for removal sites I = 1 and control sites I = 1/2.
† For control sites capture rate includes primary but excludes secondary recaptures within monthly trapping sessions.

Table 3. Generalised linear mixed models (GLMM) for the calibration of weasel footprint indices (PI) with weasel live-trapping indices (TI). Print Index scores were first transformed by taking ln (PI + 1). Covariates were defined for season (winter/spring: December-May; summer/autumn: June-November), year (year 1: March 1998 - February 1999; year 2: March 1999 - February 2000), site type (control: sites 2, 4 and 6; removal: sites 1, 3 and 5); vole density as a continuous variable (voles ha^{-1}) and temperature as mean minimum temperature (°C at grass level at 09:00 at Kielder Castle for the tracking session). All covariates are listed for the general model in italics. Only additional terms are given for alternative models. Each alternative model contained only one additional term except that including site type.

Effect of:	Coefficient of dispersion	df	F	P	Covariance of site (± SE)
General model					
PI	*0.853*	*1,102*	*4.29*	*0.041*	*0.801 ±0.579*
Season		*1,110*	*12.15*	*0.001*	
Vole density		*1,105*	*8.22*	*0.005*	
*PI * vole density*		*1,104*	*12.92*	*0.001*	
Alternative models:					
Year	0.822	1,110	8.97	0.003	0.454 ± 0.383
Site type †	0.828	1,3	1.76	0.29	0.320 ± 0.386
Temperature	0.796	1,82	3.60	0.061	0.550 ± 0.437

† Model including site type also includes year to control for unbalanced data.

cantly smaller than the coefficient for control sites (test for equality of slopes: $t = 2.33$, $df = 82$, $P = 0.011$). Indeed in removal sites weasels were caught and removed in either the first or the second week of a month in 30.7% of all weeks in which tracking took place. Therefore, in subsequent analyses the mean Print Index value for each month was used for control sites, whereas the Print Index score for each individual week was used for removal sites as, unlike control sites, there was frequently variation in actual weasel abundance between weeks within a month in removal sites.

More males than females were caught in both control and removal sites (Table 2). The Trap Index (TI) was highly significantly related to the Print Index in both control and removal sites (GLMM of the relationship between TI and PI, control sites: $F_{1,15} = 9.84$, $P = 0.007$; removal sites: $F_{1,94} = 33.64$, $P < 0.001$).

Vole densities ranged from 33 to 456 voles ha^{-1} during the period of study. As the number of weasel tracks varied with season and vole density (Graham 2001), these terms were included in the general Print Index calibration model. There was a significant year effect but when it was included in the model, neither site type nor any of its interactions with vole density and the Print Index were significant. Data from control and removal sites were therefore pooled for all the subsequent models, including the general calibration model (Table 3). Temperature had a weak though not significant effect on the relationship.

The number of weasels caught per trap day (TI) varied with season and the interaction between the Print Index and vole density (see Table 3). The interaction between the Print Index and vole density was highly significant and positive (Fig. 1). The estimate of the interaction parameter did not vary greatly with the addition of temperature, year or site type and year to the model (Table 4). The number of weasels caught per trap day estimated from the model was significantly greater in summer/autumn than in winter/spring at mean values of Print Index and vole density ($t = 3.49$, $df = 110$, $P = 0.001$; least squares means estimates: summer/autumn = 0.013; winter/spring = 0.003).

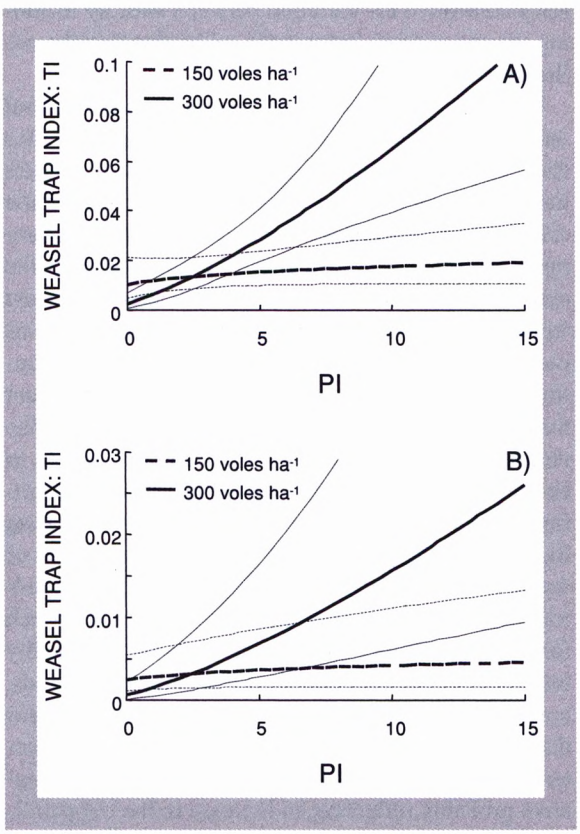

Figure 1. Calibration curves for weasel footprint indices (PI) at vole densities of 150 and 300 voles ha^{-1} in A) summer/autumn, and B) winter/spring. Fitted values (bold lines) and 95% confidence intervals (faint lines) were back transformed from the log scale parameters estimated by a GLMM.

Table 4. Parameter estimates (log scale) for generalised linear mixed models (GLMM) for the calibration of weasel footprint indices (PI) with weasel live-trapping indices (TI). The general model (in italics) is fully specified but only estimates of the PI * vole density interaction parameter are given for alternative models. The values of t and P are for the null hypothesis that a parameter equals zero. Degrees of freedom (df) for these models are specified in Table 3.

Parameter		Estimate	SE	t	P
General model:					
PI		*-0.9102*	*0.4395*	*-2.07*	*0.041*
Summer/autumn		*-3.1516*	*0.7242*	*-4.35*	*0.000*
Winter/spring		*-4.5768*	*0.6571*	*-6.97*	*0.000*
Vole density		*-0.0095*	*0.0033*	*-2.87*	*0.005*
*PI * vole density*		*0.0076*	*0.0021*	*3.59*	*0.001*
Alternative models including:					
Year	PI * vole density	0.0065	0.002	3.31	0.001
Site type & year	PI * vole density	0.0059	0.0019	3.05	0.003
Temperature	PI * vole density	0.0067	0.0023	2.98	0.004

Discussion

The number of tunnels with weasel footprints was tightly related to the number of weasels live-trapped, although the relationship varied with vole density. This relationship indicates that footprint tunnel tracking is a valuable technique for assessing weasel abundance provided factors influencing weasel density and activity, such as prey abundance and season, are corrected for. I controlled for variation between sites by including site as a random factor in the calibration thus the calibration model was not site specific.

The Trap Index was used to approximate actual weasel abundance as: 1) the small size of the study sites (5-12 ha), and consequently small number of weasels liable to be trapped, in the control sites, precluded the calculation of actual population estimates using capture-mark-recapture methods; and 2) in removal sites, the assumptions of removal methods for density estimation were not met. Moreover by using the Trap Index, it was possible to compare and then combine data from control and removal sites. Jedrzejewski et al. (1995) found trapping indices of weasel abundance, based on the number of weasels live-trapped per 100 trap-nights, to be linearly related to actual weasel density. The resulting correlation was extremely strong demonstrating that such trapping indices are reasonable predictors of actual abundance. However, Alterio et al. (1999) studied variation in stoat trappability and density in a beech forest in New Zealand. They found that stoat trappability increased in the second of their two sampling periods, concomitant with a decrease in mouse *Mus musculus* density. In the general calibration model, the parameter estimate for the main effect of vole density is negative probably reflecting an increase in the trappability of weasels at low vole density, which may have positively biased the Trap Index. Where the Print Index score was greater than zero in summer/autumn, and for all values of Print Index in winter/spring, the influence of the main effect of vole density on the predicted value of weasel abundance was minimal. However, in summer/autumn when no weasel tracks were recorded and vole density was less than approximately 125 voles per hectare, the predicted values were strongly influenced by the negative vole density parameter. For this reason, if vole density is less than 125 voles per hectare, to predict weasel abundance using the calibration equation I recommend using a minimum of 125 voles per hectare. While 125 voles per hectare appears to be a relatively high vole density to set as a minimum, it is worth pointing out that in this study both vole and weasel density were measured only in prime habitat, which constitutes only some 17-18% of Kielder Forest as a whole. If vole density were assessed at a landscape level, as is frequently the case in other studies particularly in Scandinavia, the resulting vole density would be much lower.

Factors influencing weasel density and activity

Vole density and season both influenced weasel density and/or activity during the course of the two-year study in Kielder Forest and were therefore included in the calibration model. As expected, for the same number of tunnels with weasel footprints, the actual number of weasels live-trapped was greater at high vole density. This was probably due to a decrease in weasel home range size as vole density increased. Jedrzejewski et al. (1995) found that rodent density had a profound influence on weasel density and home range size for common weasels *M. nivalis vulgaris* subject to non-cyclic fluctuations in rodent abundance in deciduous forest in eastern Poland. Moreover Jedrzejewski & Jedrzejewska (1996) observed a 17-fold increase in the mobility of male weasels corresponding to a crash in the number of rodents. In contrast they found that rodent density had little influence on weasel activity (Jedrzejewski et al. 2000). Oksanen & Henttonen (1996) did find that prey density affected activity indices of stoats in taiga habitat in Finnish Lapland: individuals were more active at

low prey densities. Therefore, it is possible that the observed variation in tracking rates was caused by variation in actual density, activity or both. Not correcting for this variation would bias estimates of weasel abundance: weasel abundance may appear to be relatively low at high prey density and conversely relatively high at low prey density. Consequently, if attempting to document the numerical response of weasels to changes in the density of their prey, it might be falsely perceived that there is a delay in the numerical response.

Korpimäki et al. (1991) similarly found between-year variation in the number of snow track-lines crossed by male least weasels *M. n. nivalis* in farmland in western Finland, where vole populations are cyclic. However, as they did not find a significant correlation between the autumn trap index of *Microtus* voles and the mean yearly number of track lines crossed by male least weasels in winter, they chose not to correct for the effect of fluctuating vole numbers in their snow-tracking indices of least weasel density.

In this study, I found that weasel density and/or activity also varied between seasons within years; therefore, it was necessary to control for this effect in calibrating the Print Index. A greater number of weasels were caught during the summer and autumn than in winter and spring, for the same number of tunnels with weasel footprints. This pattern probably reflected increased weasel numbers and the occurrence of family parties during the breeding season, as it did not match the seasonal variation in weasel activity documented in eastern Poland (Jedrzejewski et al. 2000), which would predict the opposite trend. Common weasels are capable of producing up to two litters in years of very high vole density but do not breed in winter and, although solitary for much of the year, for two or three weeks prior to independence young weasels may move around in family parties (King 1989). Similarly, although Jedrzejewski et al. (2000) found that weasel activity was strongly correlated with mean daily temperature, the effect of temperature in the calibration model was weak and did not influence the estimate of the Print Index*vole density interaction parameter. There was no evidence to suggest that the Print Index saturated or became asymptotic at the high weasel densities encountered in summer/autumn.

The parameter estimates, in particular the Print Index*vole density interaction parameter, were relatively insensitive to the inclusion of additional terms in the calibration model. This result suggests that the general calibration model was robust and can be used to reliably predict the number of weasels that will be caught per trap day. As both indices were estimated with error the regression parameters are likely to be biased although if the error in the Print Index does not vary between calibration and application data sets, this is of less consequence.

The fact that the relationship did not differ between control and removal sites reinforced the strength of the model: the effect of site type was not significant in the presence of a year effect. It was necessary to include year in the model when testing for any influence of site type to allow for the imbalance in the data, as there was no weasel trapping in control sites in the first year. The consistency of the relationship between control and removal sites indicates that the calibration model should be applicable to a wide range of situations. There was, however, a significant effect of year itself. Between-year variation may be associated with cycle phase but with only two years of data, it was not possible to reliably estimate between-year variation or determine its cause. Moreover, the inclusion of year in the model did not greatly alter the estimate of the interaction parameter. The effect of year was, therefore, not included in the general calibration model to increase its general utility. Clearly, successive data points from each site lacked temporal independence. Although I chose not to explore this, it is a potential refinement to the calibration model that might be worth exploring in the future.

All tracking tunnels remained in place throughout the study, so neophobia, or equally neophilia, was not likely to have influenced the use of tracking tunnels. Indeed a large proportion of the tunnels were used during the course of the study by a variety of species including field voles and bank voles *Clethrionomys glareolus*, wood mice *Apodemus sylvaticus*, shrews (*Sorex araneus*, *Sorex minutus* and possibly also *Neomys fodiens*), adders *Vipera berus*, common frogs *Rana temporaria*, invertebrates and on rare occasions even passerine birds. In other areas, it is possible that the use of tracking tunnels by other species, in particular stoats (Erlinge & Sandell 1988), could interfere with the tracking rate of weasels, as may be the case with rats and mice (Brown et al. 1996). However, during the two years of this study, only three stoat tracks were recorded and three stoats were caught (all in November, presumably dispersing juveniles); therefore interference was unlikely to have been a problem.

Estimating weasel abundance

By standardising the tracking effort and method some of the potential for variation in the Print Index was reduced. The strong relationship between Print Index scores in the first and second week of each month suggests that there is not much loss in accuracy by

estimating tracking rates only one week per month rather than two. In the removal sites, however, as expected there was more variation in Print Index scores between the first and second week, as sometimes, but not always, weasels were caught and removed during the first tracking week. In cases where weasel numbers are expected to be more variable, it may be beneficial to invest effort in more frequent tracking.

The habitat type was the same in all six sites, and incorporating site as a random factor in the calibration model controlled for any between-site variation. In this manner the calibration curve was robust to the assumption that weasel tracks were equally likely to be recorded in different places and different habitat types (Sutherland 1996). However, before applying the same relationship in other habitat types the assumption that tracking rates do not differ between habitat types requires testing.

This calibration was developed for unbaited tunnels arrayed in grids. In some instances, using transects of tunnels might be more efficient or baiting tunnels might be necessary. Although spatial analysis of weasel tracks did not improve the calibration (Graham 2001) suggesting that transects and grids might be equivalent for assessing weasel numbers, this idea should be tested. Female weasels typically have much smaller home ranges than males (King 1989), and the chance of not detecting a female could be greater with transects. Tracking rates were generally low during the winter and at low vole density. This problem has been overcome in other studies by baiting the tracking tunnels (Clapperton et al. 1999). I chose not to use bait as this could have introduced behavioural heterogeneity in the response of individuals to the tracking tunnels or caused variation in tracking rates over time (King & Edgar 1977, Brown et al. 1996).

These data highlight the importance of taking vole density into consideration when assessing weasel abundance by footprint tunnel tracking or other activity indices. By not correcting for prey abundance spurious patterns can emerge from data obtained using such indices. For example, in Kielder as vole numbers decline weasel numbers may appear to increase, leading to the false conclusion that there is a delay in the numerical response of weasels to changes in vole numbers. Alternatively, if monitoring weasel numbers for conservation purposes, it might be falsely concluded that weasels have exceeded the threshold limit above which their numbers require to be controlled, although this is not the case. When used with caution, however, tracking tunnel indices can be a useful tool for efficiently assessing weasel abundance.

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