

The impact of weasel predation on cyclic field-vole survival: the specialist predator hypothesis contradicted

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Summary

1. The delayed density-dependent predation of specialists such as weasels (*Mustela nivalis* L.) may result in cycles in the abundance of their prey. We estimated the demographic impact of weasel predation on field-vole (*Microtus agrestis* L.) survival using capture–recapture data from a large-scale, replicated predator-manipulation experiment conducted in six unfenced populations in Kielder Forest, northern England. The density of weasels was experimentally reduced through continuous live-trapping in the three removal populations. Field-vole survival was compared between paired removal and control populations during the increase, peak and decline phases of a vole population cycle. Apparent survival and recapture probabilities were estimated using open population Cormack–Jolly Seber models.

2. Field-vole survival varied extensively both spatially between populations and temporally, being highest in the late autumn and over winter and lowest each year in spring and early summer. Patterns of variation in male and female survival were similar between populations over time, but there was independent spatial and temporal variation between adults and juveniles. Variation in weasel abundance explained 18% of this independent spatial and temporal variation between adult and juvenile field-vole survival.

3. The average increase in annual vole survival resulting from weasel removal over the 2-year period was 27% and 25% for adult male and female field voles, respectively. Decreased weasel abundance increased adult field-vole survival. Adult-vole survival in the absence of weasels was predicted to be approximately 8% higher than in the presence of one weasel per 4–5 ha. Surprisingly, weasel removal resulted in lowered juvenile field-vole survival, possibly reflecting increased emigration or mortality due to infanticide. A simple two age-class demographic model indicated that the decrease in juvenile survival in response to reduced weasel predation pressure did not fully compensate for the increase in adult survival.

4. As weasel numbers fluctuated seasonally, with highest weasel densities occurring in late summer and autumn and little spring to spring variation, the impact of weasel removal on field-vole survival was greatest during the breeding season. However, vole population-growth rates were unrelated to adult survival at that time and correspondingly no divergence was observed between the trajectories of control and removal vole populations even when weasel numbers were greatest in control sites. In contrast, vole population-growth rates were closely correlated with survival during the non-breeding season. Nevertheless all control and removal populations experienced a cyclic decline in winter 1999–2000 in spite of the increased adult survival in experimental treatments.

5. We conclude that the impact of weasel predation on field-vole survival was neither sufficient nor necessary to initiate and drive the cyclic decline of field-vole populations in Kielder Forest.

Key-words: capture–recapture, compensation, field voles, MARK, *Mustela nivalis*, population cycles, specialist predators.

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Introduction

The potential impact of predators on prey populations is an important and often controversial issue of interest not just to ecologists. For example the impact of alien predators on native fauna worldwide is currently a main conservation concern (e.g. O'Donnell 1996). Predators can influence their prey populations directly through mortality but indirect effects may also occur through the suppression of reproduction in prey species (for review see Lima & Dill 1990). Another recurrent theme in predator-prey dynamics is the 'Erringtonian' view that predation merely falls on a doomed surplus of individuals. Whether or not predators select individuals of a specific age-class or sex or health might affect the magnitude of their impact on the prey population (Caro & FitzGibbon 1992).

Cyclic fluctuations in populations of small mammals have stimulated a great deal of research and debate in ecology (e.g. Stenseth 1999). The specialist predator hypothesis, that mammalian specialists, in particular weasels, are responsible for driving population cycles of microtine rodents (Andersson & Erlinge 1977), has been perceived as the probable explanation for the cause of vole population cycles (Korpimäki & Krebs 1996; Hanski *et al.* 2001). Yet few of the studies on population cycles of voles have demographic data on the impact of predation on voles. We tested the specialist predator hypothesis experimentally by conducting a long-term, large-scale, replicated weasel removal experiment during the increase, peak and decline phases of a vole population cycle in northern England (I. M. Graham & X. Lambin unpublished data). Elsewhere, we presented the 'numerical' results of our weasel removal experiment, specifically the changes in the size and growth rate of vole and weasel populations. We found that reducing weasel predation pressure had no impact on the size and growth rates of experimentally manipulated field vole populations in Kielder Forest. However, as fluctuations in population size and growth rate result directly from changes in demographic variables, it is equally important to consider the mechanisms underlying the numerical patterns observed, particularly following an experimental manipulation (Krebs 1996; Yoccoz *et al.* 1998; Oli & Dobson 1999). This is all the more important given the necessarily limited replication and imprecise nature of large-scale experiments such as ours (May 1999; Lambin *et al.* 2002). Quantifying the demographic changes can (a) validate and help to explain the observed results, (b) be useful for making predictions, e.g. in predicting the response to a greater treatment effect, and (c) be used to generate estimates of parameters for simulation models.

There have been very few large-scale, predator removal experiments conducted to test the role of predation in regulating population cycles of microtine rodents and almost all have been carried out using fenced enclosures (e.g. Klemola *et al.* 2000). A notable exception is the predator removal experiment carried

out in six unfenced areas (2–3 km²) in two years (1992 and 1995) during the crash phase of the vole cycle in western Finland by Korpimäki, Norrdahl, Klemola and colleagues (Klemola *et al.* 1997; Korpimäki & Norrdahl 1998). However, Korpimäki and colleagues used snap-trapping methods to monitor the small mammal populations; consequently they could say little about the demographic changes which caused an increase in vole numbers in manipulated areas only in 1995.

Most previous studies have tested the role of predation in regulating the population dynamics of small mammals in enclosures (Korpimäki & Krebs 1996). Both Erlinge (1987) and Reid, Krebs & Kenney (1995) observed increased survival rates in populations, of voles and lemmings, respectively, protected from predation, but attributed the failure of protected populations to grow to dispersal of individuals outside the fenced area where they suffered high mortality. Desy & Batzli (1989) also found increased survival in enclosed vole populations protected from predation, and found in addition that protected populations reached higher densities; however, the enclosures used were impermeable to voles such that any compensatory effect of dispersal could not be examined. Klemola *et al.* (2000) also used enclosures that prevented vole dispersal and similarly reported rapid population growth to high density in the enclosed vole populations, although they do not report any of the demographic variables for the enclosed populations. The difficulty with such enclosure experiments lies in knowing to what extent fences disrupt the demographic processes of enclosed populations, and to what degree the results are applicable to natural populations.

Several studies, including our own in Kielder Forest, have shown that weasels can be a major cause of mortality in voles (Jedrzejewski, Jedrzejewska & Szymura 1995; Norrdahl & Korpimäki 1995; X. Lambin *et al.* unpublished data). We therefore investigated the influence of removing weasels on field-vole survival in the increase, peak and decline phases of a vole population cycle in northern England. We tested the specific predictions that experimental suppression of weasel numerical response would (1) increase survival of adult female voles, and (2) increase survival of juvenile voles (and therefore enhance juvenile recruitment). To do this, we investigated the factors, both individual (sex and age) and external (treatment and weasel abundance), influencing survival in all six vole populations during the increase, peak and early decline phases of the cycle.

Methods

The experiment was carried out in three paired treatment and control clear-cut sites (5–12 ha) in Kielder Forest, northern England (55°13'N, 2°33'W), a large man-made spruce forest. The three treatment sites are referred to throughout as removal sites. Field-vole

populations found in the grass-dominated clear-cuts exhibit three to four-year cyclic dynamics similar in many respects to those in central Fennoscandia. A detailed description of the study area is found in Lambin, Petty & MacKinnon (2000). Removal and control sites were separated by between 2 and 4 km as, in Kielder, at distances greater than 4 km vole populations tend to have asynchronous dynamics (Lambin *et al.* 1998); however, the pairs themselves were greater than 4 km apart.

From April 1998 onwards, weasels were live-trapped and removed from the three removal sites to suppress their numerical response. Weasels were removed from the entire clear-cut in each case. Twenty-five wooden box traps, built to the design specifications of King (1973), were set for an average of 6.5 ± 0.5 nights per month at each site. Traps were baited with previously frozen fish and checked at 24-h intervals. All weasels were ear-tagged, translocated from Kielder and released in similar habitat a minimum of 10 km from the initial capture site. No weasels were ever recaptured following translocation. A total of 80 weasels were removed from all three removal sites from May 1998 to May 2000 (Graham 2001).

In order to establish the efficiency of the weasel removal on removal sites and quantify weasel numerical response on control sites, weasel abundance was assessed at all sites using footprint tunnel tracking. Footprint tracking was carried out at five of the six sites from April 1998 to April 2000, and at the sixth from July 1998 to April 2000 excluding November 1998, according to the method described by King & Edgar (1977). For a detailed description of the methods see Graham (2002). The weasel Trap Index (TI) was derived from the number of tunnels in which weasel footprints were recorded in any given week using a calibration equation to correct for the effect of vole density on weasel density and activity (Graham 2002). In 1999, weasel abundance was reduced by an average of 57 and 60% in mid-summer and autumn, respectively, in each of the three removal sites (Graham 2001). The TI was the measure of weasel abundance used as a covariate in vole survival analyses.

Field-vole populations were trapped every month, March–October 1998, 1999 and March–May 2000, at all six sites by capture–recapture methods. Each site had a permanent live-trapping grid (0.3 ha) consisting of 100 Ugglan Special Mousetraps (Grahnb, Marieholm, Switzerland) set at 5-m intervals, which were baited with wheat and carrots. Traps were prebaited 2–3 days before each live-trapping session, then set at approximately 18:00 h on the first day. From March 1998 to March 2000 inclusive, traps were checked five times at roughly 12-h intervals, dawn and dusk. From April 2000, and at two sites in April 1998 when trapping was aborted owing to adverse weather conditions, traps were checked only three times. Voles were marked with uniquely numbered Hauptner ear-tags (Hauptner & Herberholz, Solingen, Germany) on the occasion of their first capture,

either as adults or juveniles, and their mass and reproductive status noted at the time of first capture each month (primary session). During the study, vole densities ranged from 33 to 456 voles ha^{-1} (Graham 2001).

Field voles were categorized as ‘juvenile’ or ‘adult’ based on their fur: individuals with juvenile fur or in their first moult were classified as juveniles. Therefore ‘juveniles’ according to our classification would be less than 4 weeks old. Recruitment rates were calculated as the number of juveniles trapped in a given month per adult female in the previous month. Individuals recaptured having lost their tags were identified according to sex, mass, reproductive status, capture location or any other distinguishing feature. In most cases, this produced an entirely satisfactory match and should serve to avoid the negative bias in survival resulting from tag loss (Diefenbach & Alt 1998).

SURVIVAL ANALYSES

We estimated apparent survival and recapture probabilities in standard open population Cormack–Jolly Seber models (Lebreton *et al.* 1992) implemented in MARK (Cooch & White 1999; White & Burnham 1999). The full data set comprised the capture histories of 2576 field voles (683 females and 1020 males marked as adults and 430 females and 443 males marked as juveniles). Survival and recapture probabilities quoted in this paper refer to the probability of survival or recapture for a 28-day period: the longer over-winter intervals between trapping sessions were taken into account in the survival analysis. Our model selection strategy, as recommended by Lebreton *et al.* (1992), was as follows. (1) An appropriate, biologically meaningful global model was selected and its fit verified. (2) Variation in recapture rates was modelled before constraining variation in survival to increase the power of detecting variation in survival rates. (3) Parsimonious models capturing the time dependency in survival were selected on the basis of AICc (Akaike’s Information Criterion) (Anderson, Burnham & Thompson 2000). (4) *A priori* predictions for the experiment were tested using likelihood ratio tests on selected models. The modified criterion, AICc, was used for model selection, as the number of parameters estimated by models was large relative to the sample size (Anderson *et al.* 2000). AICc was calculated as $\text{AIC} = (-2 \times \log\text{-likelihood} + 2 \times \text{no. parameters})$ corrected for the effective sample size. Model notation is explained in Tables 2 and 3.

The CMR models used assume that: (1) every marked animal in the population immediately after time (t) has the same probability of surviving to time ($t + 1$); and (2) every marked animal present in the population at time (t) has the same probability of recapture (p). We therefore carried out an initial goodness-of-fit (GOF) test on the global (most fully parameterized) model, $\phi_{a2*s*g*t} p_{a2*s*g*t}$ (with both survival and recapture probabilities dependent on age, sex, site and time), using RELEASE (Burnham *et al.* 1987), in MARK.

Table 1. Modelling age, sex and temporal variation in field-vole survival for individual sites in Kielder Forest. The selected model and model with additive age, sex and time effects (ϕ_{s+a2+t}) are shown for each site. The recapture model used in the model selection procedure for all sites was p_{a2} . Variance-covariance matrices were estimated using the Hessian procedure in MARK. Additive models including the main effects only are indicated by a plus sign (+); specific interactions are symbolized by a dot (·); models including all the interactions are represented by an asterisk (*)

Site	Treatment	Model	Survival model†	Deviance	No. of parameters	AICc (Δ AICc)
1	Removal	Selected	$\phi_{s+a2+a2*t}$	433.5	40	1462.7
			ϕ_{s+a2+t}	476.5	22	1466.9 (4.3)
2	Control	Selected	ϕ_{s+a2+t}	296.9	22	1022.4
3	Removal	Selected	$\phi_{s+a2*(m+y)}$	435.7	23	1370.6
			ϕ_{s+a2+t}	445.5	22	1378.3 (7.6)
4	Control	Selected	ϕ_{a2+m+y}	262.2	13	657.8
			ϕ_{s+a2+t}	249.1	22	664.4 (6.7)
			ϕ_{s+a2+m}	470.4	12	1483.6
5	Removal	Selected	ϕ_{s+a2+t}	458.7	22	1492.7 (9.1)
			ϕ_{s+m+y}	464.9	13	1715.6
6	Control	Selected	ϕ_{s+a2+t}	451.3	22	1720.6 (5.0)

†Subscript meanings: s: sex; a2: two age classes (juvenile and adult); t: full time-dependence (session-to-session variation); m: monthly time-dependence; y: yearly time-dependence.

The GOF test for the whole data set, split by age at first capture, sex and site, was not significant suggesting that the fit of the model was acceptable (Test 2 and 3, RELEASE: $\chi^2 = 248.80$, d.f. = 401, $P = 1.00$). However, Test 2.C in particular had very few degrees of freedom because of the sparseness of the data. We therefore examined the contingency tables (pooled within site) for Tests 3.SR and 2.CT produced using RELEASE (Burnham *et al.* 1987), as modified by Pradel (1993) for a systematic bias, i.e. an excess of tables in which the cells on one or other diagonal exceed the expected frequencies. We performed sign tests (Sokal & Rohlf 1995) on the frequency of contingency tables with a particular bias. Using this method, Tests 2.CT and 3.SR were marginally significant for one site only, site 6 (Test 2.CT: $t = 3.00$, d.f. = 8, $P = 0.01$; Test 3.SR: $t = 2.10$, d.f. = 50, $P = 0.05$). However, given the number of sequential tests, this could be due to experimentwise error rate; moreover for this and three other sites the sample size for Test 2.CT was unsatisfactory (Sokal & Rohlf 1995). Where the number of individual contingency tables examined exceeded 12, there was no evidence of lack of fit. We therefore started in the analysis with $\phi_{a2*s*g*t}$ $p_{a2*s*g*t}$ as our global model. In order to simplify the model-selection procedure and identify a reduced set of realistic models, we initially modelled variation in recapture and survival with age, sex and time using the data sets for individual sites. We fitted all additive combinations of p with age, sex and time (fully time-dependent and constrained time-dependent: season and year) and all combinations of ϕ with age, sex and time to the data sets for individual sites. We then identified a suitable, reduced starting model for the data set for all sites. To test our predictions on the effect of the experimental treatment (removal of weasels) on survival, we fitted models including treatment coded either as: (1) a categorical variable (removal or control) or (2) an external, continuous covariate (coded as the difference between mean weasel abundance during

each period in paired control and removal sites). To incorporate our experimental design when fitting these models, we included a pair * time interaction term. Finally, to investigate the influence of weasel abundance on vole survival in all sites, we used the site-specific mean weasel abundance during each period as an external, continuous covariate. The amount of variation explained by using weasel abundance as a covariate was calculated by analysis of deviance (Skalski, Hoffman & Smith 1993):

$$\text{Amount of variation explained} = \frac{[\text{deviance (constant model)} - \text{deviance (covariate model)}]}{[\text{deviance (constant model)} - \text{deviance (time \& group-dependent)}]}$$

Results

SURVIVAL MODEL SELECTION

Individual sites

Models with a lower recapture rate for juveniles than adults fitted the data better than models assuming recapture rates to be the same for both age classes. Including variation in recapture between males and females, however, did not reduce the AICc of models. There was no indication that recapture rates would be better modelled by incorporating independent temporal variation between ages or sexes, i.e. the selected models included either no or only additive/parallel time-variation of recapture rates between groups. Indeed, it was more acceptable in terms of AICc to constrain time to vary between seasons ('early' breeding season, March–June, and 'late' breeding season, July–October) and/or years than to include full temporal variation between trapping sessions.

All the selected models included temporal variation in survival (Table 1). For two removal sites, temporal variation in survival was best modelled independently

Table 2. Modelling the impact of weasel predation on field-vole survival for all sites in Kielder Forest. The recapture model used in the model selection procedure was $p_{a2+pr+t}$ (except for the global model for which $p_{a2*s*g*t}$ was used). Variance–covariance matrices were estimated using the 2nd Part procedure in MARK (apart from the global model). Estimates of the age class * weasel abundance interaction parameter are on a logit scale. Selected models are highlighted in bold

Model no.	Model†	No. of parameters	Deviance	AICc	Parameter estimate for a2.mw ± SE
Global model					
	$\phi_{a2*s*g*t}$	~863	1711.2	~8909.2	
General models					
1.	$\phi_{s+a2*g+a2*t+g*t}$	147	2286.8	7684.8	
2.	$\phi_{s^g+a2^g+a2^t+g*t}$	152	2282.3	7691.0	
3.	$\phi_{s^t+a2^g+a2^t+g*t}$	164	2257.1	7691.4	
4.	$\phi_{a2^g+a2^t+g*t}$	146	2307.0	7702.8	
5.	$\phi_{s+a2^*mw+g*t}$	131	2340.4	7704.4	-0.211 ± 0.074
6.	$\phi_{s+a2+g*t}$	130	2352.6	7714.5	
7.	$\phi_{s+a2^g+a2^*(m+y)+g^*(m+y)}$	94	2437.4	7723.8	
8.	$\phi_{s+a2^g+a2^t+pr*t}$	96	2448.9	7739.5	
9.	$\phi_{s+a2^g+a2^t}$	62	2524.9	7745.2	
10.	$\phi_{s+a2+pr*t}$	76	2517.9	7767.1	
11.	ϕ_{s+a2+t}	40	2595.1	7770.4	
12.	ϕ_{s+a2^g}	34	2964.0	8127.2	
13.	$\phi_{s^g+a2^g}$	185	2208.8	7688.3	
Analysis of treatment (categorical)					
14.	$\phi_{s+a2^*t+trt^*t+pr^*t}$	107	2418.8	7732.3	
15.	$\phi_{s+a2^*t+a2^*trt+trt^*t+pr^*t}$	108	2417.3	7732.9	
16.	$\phi_{s+a2^*t+trt+pr^*t}$	89	2475.0	7751.1	
17.	$\phi_{s+a2^*t+pr^*t}$	88	2476.8	7750.8	
Analysis of treatment (difference in weasel abundance)					
18.	$\phi_{s+a2^*dw+pr^*t}$	78	2507.7	7760.9	
19.	$\phi_{s^*dw+a2^*dw+pr^*t}$	79	2506.0	7761.3	
20.	$\phi_{s^*a2^*dw+pr^*t}$	81	2504.5	7763.9	
21.	$\phi_{s+a2+dw+pr^*t}$	77	2517.4	7768.6	
Effect of mean weasel abundance					
22.	$\phi_{s+a2^*mw+pr^*t}$	78	2503.3	7756.6	-0.222 ± 0.072
23.	ϕ_{s+a2^*mw+m}	32	2602.0	7761.1	-0.191 ± 0.060
24.	ϕ_{s+a2^*mw+t}	42	2583.1	7762.5	-0.180 ± 0.062
25.	$\phi_{s^*a2^*mw+m}$	35	2596.7	7761.8	
26.	$\phi_{s^*mw+a2^*mw+m}$	33	2601.6	7762.7	
27.	$\phi_{s+a2+mw+m}$	31	2614.9	7772.0	

†Additional subscript meanings not explained in Table 1: pr: site pair – 3 levels; g: site (grid) – 6 levels; trt: experimental treatment – weasel removal (control and removal); dw: difference in mean weasel abundance between paired sites; mw: mean weasel abundance at individual sites.

for juveniles and adults: models with the lowest AICc values included an age * time interaction. However, for the other four sites, models assuming consistent (additive) temporal variation between groups were acceptable. The difference in survival between sexes appeared to be constant between age classes. For all six sites, the only model for which AICc consistently differed from the selected model for that site by less than 10 was ϕ_{a2+s+t} . Given that the selected models included an age * time interaction for two out of six sites, we chose $\phi_{g^*[s+(a2^*t)]}P_{g^*[a2+t]}$ as our starting model for the full data set.

Full data set

Although temporal variation in recapture rate could be reduced to only seasonal variation with more complex survival models, this was not the case when survival

was more constrained. To avoid over-constraining temporal variation in recapture rates and potentially reducing the power of tests and the precision of survival estimates (Julliard *et al.* 1999), we retained full additive temporal variation in recapture models with the full data set. As with the data sets for individual sites, recapture rates were best modelled by assuming a higher recapture rate for adults than juveniles but no difference in recapture between the sexes: juvenile recapture rates were on average 11% less than adult recapture rates (estimates derived from model 1 in Table 2). There was no evidence to suggest that temporal variation in recapture rate differed among the six different sites or that the effect of age on recapture rate varied among sites. Recapture rates were better modelled by including an effect of site pair. The average recapture rates for adults were 85.8%, 91.7% and 88.5% for the three site pairs,

respectively (estimates derived from model 1 in Table 2). Only 13.0% of adult recapture rates were less than 80%.

Field-vole survival varied extensively both spatially between sites and temporally (Table 2). Temporal variation was not consistent between sites (model 9 vs. model 1, $\Delta\text{AICc} = 60.4$), and could not be constrained to only additive month and year variation (model 7 vs. model 1, $\Delta\text{AICc} = 39.1$). Similarly, the spatial variation between sites could not be explained simply by variation between site pairs (model 8 vs. model 1, $\Delta\text{AICc} = 54.7$). Including independent temporal variation between individual sites, however, requires the estimation of a very large number of parameters relative to the amount of data. The residual temporal variation explained by using constant temporal variation for all sites or separately for each pair of sites was large (models 8, 9 vs. model 12, $\chi^2_{62} = 515.15$ and $\chi^2_{28} = 439.14$, respectively), suggesting that much of the temporal variation was common to all sites. As a compromise we therefore used these simpler models to estimate survival probabilities. We verified that simplifying temporal variation did not alter the influence of weasel abundance on vole survival rates and found that the models were qualitatively unaffected.

Both sexes showed similar patterns of survival between grids and temporally (models 2, 3 vs. model 1, $\Delta\text{AICc} = 6.2$ and 6.6 , respectively). Females had consistently higher survival rates (model 1 vs. model 4, $\Delta\text{AICc} = -18.1$): adult female and juvenile female survival rates estimated from model 1 were on average 5.3% and 4.9% higher than adult and juvenile male survival rates, respectively. The pattern in survival between age classes, however, was more complicated. The selected general model for survival, before consideration of experimental effects, included independent temporal variation between adults and juveniles and also independent variation in adult and juvenile survival between grids ($\phi_{s+(a2^*g)+(a2^*t)+(g^*t)}$). Adult survival rates estimated from the best general model (model 1 in Table 2) ranged from 14.7% to 92.8% per 28 days. There appeared to be a roughly similar, although not entirely consistent, seasonal pattern in the variation in survival in all sites. Survival rates were generally highest in the late autumn and over winter, and then decreased in spring to reach a seasonal low between May and July before increasing again.

IMPACT OF WEASEL REMOVAL ON SURVIVAL

Having selected appropriate models to incorporate the variation in survival and recapture rates with age, sex, time and space, we tested the hypotheses that weasel removal and weasel abundance influenced field-vole survival in our experiment. There was a significant effect of treatment, coded either as a categorical variable or as a continuous variable (difference in weasel abundance between paired sites), on vole survival. The best model with 'treatment' as a factor

included an age * time and treatment * time interaction ($\phi_{s+(a2^*t)+(trt^*t)+(pr^*t)}$): model 14 in Table 2. As expected from the variation in weasel abundance, when modelled as a categorical variable, the effect of treatment was not constant over time (model 14 vs. model 17 $\chi^2_{19} = 58.02$, $P < 0.001$). Overall vole-survival rates were greater in weasel removal than control sites. The average increase in 28-day survival rates due to weasel removal over the 2-year period was 2.24% and 2.10% for adult males and females and 0.57% and 0.78% for juvenile males and females, respectively, equivalent to an increase in annual survival rates of 26.9% and 25.2% for adult males and females and 6.8% and 9.4% for juvenile males and females. However, the effect of the treatment varied over time, thus while adult survival was on average 10.7% greater in removal sites in May 1999, the reverse was true in August when adult survival rates predicted by the model were actually greater in control sites by an average of 7.5%.

Although the three-way interaction between age, treatment and time was not significant, the significance of both an age * time and a treatment * time interaction in model 14 implied that there was an interaction between the effects of treatment and age class on survival. The difference in weasel abundance between paired sites incorporates the temporal variation of the treatment, therefore removing the need to consider interactions between treatment and time (which given the large number of time intervals introduces a large number of parameters decreasing the parsimony of the models and reducing the power to detect effects). Indeed, when we tested the relationship between survival and weasel-removal treatment directly, using the difference in weasel abundance between paired sites, we found that the effect of reducing weasel abundance did differ between age classes (model 18 vs. model 21, $\chi^2_1 = 9.77$, $P = 0.002$). However, there was no difference in the treatment effect between sexes or combined sex and age class (Table 2). To investigate this further we used actual mean weasel abundance for each site.

Weasel abundance explained 18% of the independent spatial and temporal variation in survival between age classes, although as expected the model did not fit the data as well as the best general model, model 1 (model 5 vs. model 6, $\chi^2_1 = 12.15$, $P < 0.001$; model 5 vs. model 1, $\Delta\text{AICc} = 19.7$). The interaction between weasel abundance and age class held regardless of how spatio-temporal variation was modelled (model 5 vs. model 6, $\chi^2_1 = 12.15$, $P < 0.001$; model 23 vs. model 27, $\chi^2_1 = 12.88$, $P < 0.001$), in all cases, adult survival was negatively influenced by increasing mean weasel abundance. In addition, the coefficient for the interaction term between age and weasel abundance was robust and very similar for different models (Table 2). Weasel abundance had a negative effect on adult field-vole survival but an apparently positive effect on juvenile survival (Figs 1 and 2). At a weasel abundance of 0.04 weasels trap⁻¹ day⁻¹ (corresponding to four weasels

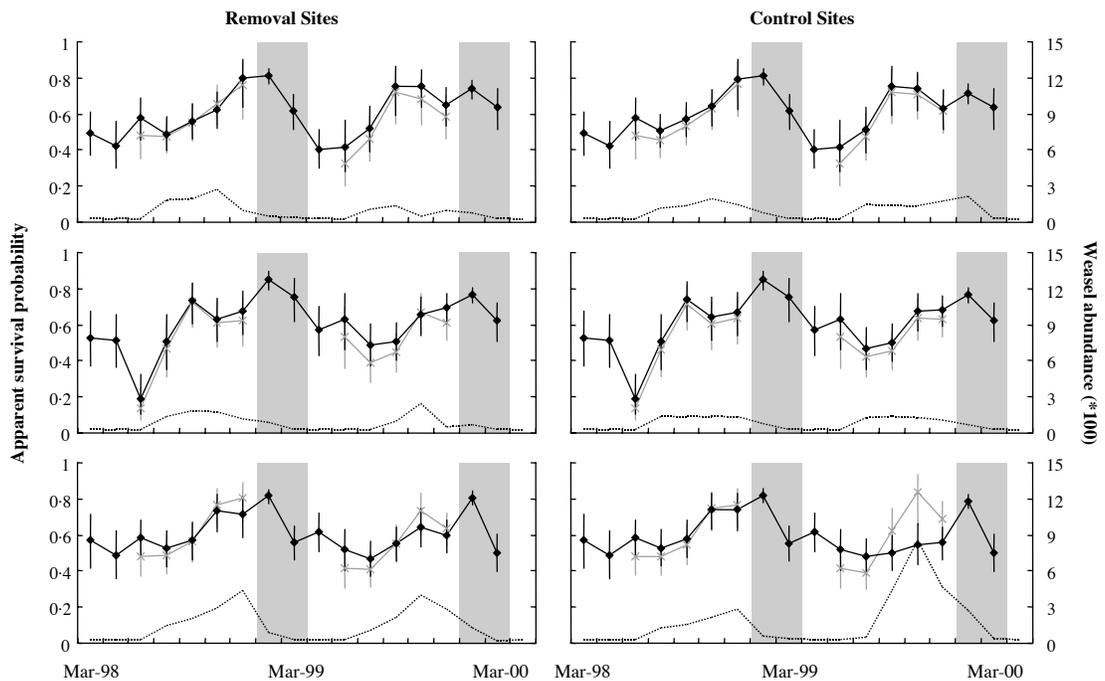


Fig. 1. Weasel abundance (weasels caught per trap day) and apparent survival probability of male field voles in the three control and removal site pairs in Kielder Forest, northern England, March 1998–April 2000. Graphs on the left are removal sites; graphs on the right are control sites; site pairs are adjacent. Black line: adult voles; grey line: juvenile voles; dotted line: weasel abundance. Shaded bars represent non-breeding season, October–April. Estimates of field vole apparent survival probability are shown with 95% confidence intervals for model $\phi_{s+a2*mw+pr*t} P_{a2+pr+t}$.

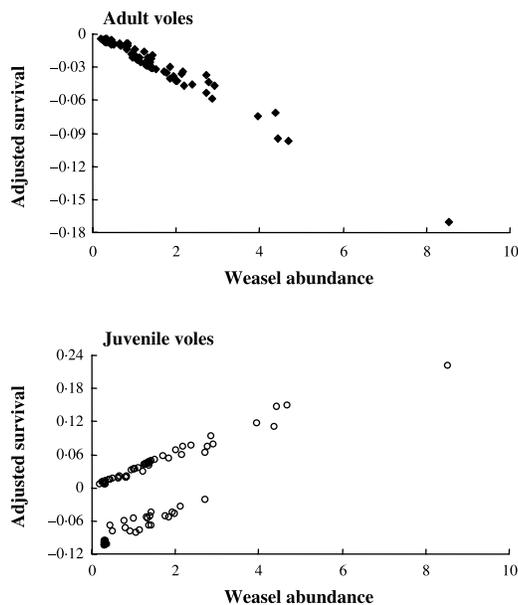


Fig. 2. Relationships between field-vole survival and weasel abundance ((weasels caught per trap day) * 100) for (a) adults and (b) juveniles predicted from the model $\phi_{s+a2*mw+pr*t} P_{a2+pr+t}$. Probability of survival was adjusted for variation in other factors. Filled diamonds: adults; open circles: juveniles.

caught per 100 trap nights or roughly one weasel per 4–5 ha), the predicted value of adult survival was approximately 8% less than in the absence of weasels. We tested whether or not this interaction was largely a consequence of the effect of weasel predation on adults or juveniles alone, by constraining only adult or juvenile

survival to vary with weasel abundance. However the model with the full interaction explained more of the variation in survival between age classes although the deviances of all three models were similar (model 22, $\phi_{s+a2+(A.mw)+(pr*t)}$, $\phi_{s+a2+(J.mw)+(pr*t)}$, vs. model 10, change in deviance = -14.61 , -11.33 and -11.81 , respectively). Moreover, the parameter estimates for the interaction of weasel abundance and adult or juvenile survival were consistent with the negative effect on adults and positive effect on juveniles predicted by model 22. Therefore, we concluded that the impact of weasel abundance on vole survival was negative for adults and positive for juveniles.

As with the difference in weasel abundance, there was no evidence to suggest that weasel abundance affected male and female survival differently (model 26 vs. model 23, $\chi^2_1 = 0.41$, $P = 0.52$). Nor did the effect of weasel abundance differ between both sex and age classes (model 25 vs. model 23, $\chi^2_3 = 5.36$, $P = 0.15$).

RECRUITMENT, GROWTH AND SURVIVAL

In order to examine the relative importance of survival and recruitment to population growth, particularly during the breeding season, we examined the relationships between survival, recruitment and population growth rates. Mean *per capita* recruitment rate (defined as the number of juveniles at time $(i + 1)$ per adult female at time (i)), April–October, was positively correlated with mean apparent survival of adult females, March–September ($r_p = 0.66$, $n = 12$, $P = 0.020$).

Mean population growth rate, April–October, was correlated with recruitment rate ($r_p = 0.54$, $n = 12$, $P = 0.070$) but not with mean adult survival during the same period ($r_p = 0.33$, $n = 12$, $P = 0.30$). There was however, a strong positive correlation between mean population growth rate and mean adult survival overwinter, from October to April ($r_p = 0.85$, $n = 12$, $P < 0.001$).

Discussion

Our experiment demonstrates that adult field-vole survival can be increased by experimentally reducing weasel-predation pressure. Weasel numerical response was suppressed in removal sites, particularly in summer and autumn 1999, yet the vole populations in all sites declined to low density and there was no consistent divergence in population trajectories between control and removal sites, in the increase, peak or decline phases of the cycle. Examining the impact of weasel predation on vole survival provides a partial explanation for this.

The models we used to investigate the impact of the treatment (weasel removal) on field-vole survival incorporated the experimental design through the inclusion of a pair * time interaction term. Although this term did not fully explain all the independent temporal variation between sites, i.e. the models had greater AIC values and were therefore less parsimonious than the best model, they were nevertheless the only appropriate models for testing *a priori* hypotheses on the impact of the experiment on field-vole survival. Our analysis of the impact of actual weasel abundance on field-vole survival shows that the poorer fit of models incorporating the experimental design did not influence the interpretation of the results. However, the percentage of variation explained by doing so was large. Moreover the age class * weasel abundance interaction parameter was robust to how the independent temporal variation between sites was modelled. It was therefore appropriate to estimate survival probabilities using the simpler models as there were insufficient data to estimate the large number of parameters required by the models incorporating full independent temporal variation among all six sites.

While weasel predation accounted for up to 20% of the variation in vole survival at high weasel abundance, weasel densities were rarely high enough to cause such an impact. Indeed, the seasonal dynamics of the weasel population and absence of year-on-year changes in their abundance (I. M. Graham & X. Lambin unpublished data) in Kielder Forest, mean that, apart from a few months in summer, weasel predation explained only 5% or less of the variation in field-vole survival. This was exemplified by the extensive spatio-temporal variation in survival rates in our six sites that could not be explained by weasel abundance. A number of previous studies have estimated weasel predation rates on rodents to be 1–35% (MacLean *et al.* 1974; King 1980;

Delattre 1984; Jedrzejewski *et al.* 1995). Although weasel predation rates cannot simply be translated into vole survival rates, it is striking that our estimate of the impact of weasel predation on field-vole survival is of a very similar order of magnitude.

The seasonal dynamics of weasels also constrained the scope for the experimentally induced contrast between treatments. However only where treatment was coded as a categorical variable was there any assumption concerning the success of the experiment. Where actual weasel abundance was used, whether the difference between paired sites or site-specific, there was no dependence on a permanent or strong difference in weasel abundance between treatment and control sites. Moreover, our conclusion on the impact of weasel predation on vole survival held regardless of the way in which variation in weasel abundance was modelled: removal vs. control, difference in weasel abundance between paired sites or site-specific weasel abundance. Given that the results of all three different approaches concurred our conclusion is strengthened.

Although population growth was strongly correlated with adult survival in the non-breeding season over winter, the relationship between growth and survival was very much weaker during the summer. Consequently, when the effect of suppressing weasel numerical response on vole survival is greatest, increasing survival might be expected to have little influence on the population growth rate other than indirectly, through the effect of increased female survival on recruitment rate. This seems to have been the case as population growth rates showed no consistent divergence between control and removal vole populations even in summer (I. M. Graham & X. Lambin unpublished data). Our results concur with the conclusions of Oli & Dobson's (1999) modelling study. Using a demographically based model, they tested the potential influence of a number of parameters, including juvenile and adult survival, on population cycles and concluded that changes in adult survival were neither necessary nor sufficient to generate population cycles.

Increased survival rates have been observed in populations of voles and lemmings protected from predation in enclosures in several previous studies (Erlinge 1987; Desy & Batzli 1989; Reid *et al.* 1995; Wilson, Krebs, & Sinclair 1999); however, our experimental results are unique in two aspects. We manipulated only weasel densities, and our experimental populations were unfenced. Where the enclosures used were permeable, the failure of such protected populations to grow has often been attributed to the relatively small size of the enclosures, often too small to encompass dispersal. Consequently, as individuals, which disperse or live outside the fenced areas, are exposed to high levels of predation, emigration may increase as a result of the disparity in densities inside and outside the enclosures. Thus Reid *et al.* (1995) postulated that the number of potential immigrants was reduced, resulting in a bias in dispersal of individuals out of the enclosures and

Table 3. The impact of changes in adult and juvenile field-vole survival rates on monthly population-growth rates (λ). Population-growth rates were estimated using a standard two age-class Leslie matrix model

Adult survival	0.63	0.73
Juvenile survival		
0.56	0.90	0.98
0.66	0.94	1.01

Erlinge (1987) reported that individuals whose home ranges extended outside the enclosure suffered high mortality rates. The surprising result of our study, that juvenile survival decreased in response to the reduction in weasel-predation pressure, suggests, however, that the lack of population growth might not have been an artefact of using enclosures. In our experiment, weasels were removed from entire clearcuts therefore vole populations in removal sites were not in direct contact with vole populations at lower densities. Nevertheless, juvenile survival decreased when weasel-predation pressure was reduced. This decrease in juvenile survival may have partially compensated for the increase in adult survival, contributing to the lack of divergence between vole population trajectories in control and removal sites, even when control sites experienced much higher levels of weasel predation. We used a simple standard age-based Leslie matrix model to explore the idea that the decrease in juvenile survival in response to reduced weasel-predation pressure did compensate for the increased adult survival. We used appropriate estimates of juvenile and adult survival suggested by model 22 and used a two age-class model. In spite of all the simplifying assumptions of this approach, it illustrates that the similar, although opposite, effects of weasel abundance on juvenile and adult survival were probably not fully compensatory (Table 3).

Suppression of the weasel numerical response increased adult vole survival in removal sites but it effectively reduced juvenile survival. As apparent survival probabilities confound dispersal and mortality, this decrease in juvenile survival could have been simply due to increased mortality or alternatively to increased emigration. In removal sites, it is possible that the higher number of adults in the population caused more juvenile mortality through infanticide. Instances of infanticide have been reported in some vole species (e.g. Boonstra 1978; Lidicker 1979; Caley & Boutin 1985) and infanticide has been shown to contribute significantly to juvenile mortality in Townsend's voles (*Microtus townsendii*) (Lambin & Yoccoz 1998). This same study demonstrated quantitatively that nestling survival was significantly lower in areas where the relatedness among females was lower (their low-kinship treatment), which they attributed to increased infanticide.

Higher numbers of adults may, however, have caused increased juvenile dispersal by forcing juveniles to disperse greater distances and making it difficult for juveniles to settle and recruit into the population. Julliard *et al.* (1999) similarly found a negative effect of multimammate rat (*Mastomys natalensis*) density on survival of newly marked subadults, whereas the effect of rat density on adults and previously marked subadults was positive. A possible solution to the paradox of lower juvenile survival in spite of equal densities may lie with the change in population age-structure that would result from increased adult survival. Pusenius & Viitala (1993) found that field-vole spacing behaviour in wild populations showed pronounced variation, which they attributed to differences in behaviour related to age and social dominance. They found that the old, over-wintered females became increasingly territorial as the breeding season progressed, whereas the younger females had much smaller, more extensively overlapping home ranges even when reproducing. Similarly, Agrell *et al.* (1995) found that female field voles were more territorial in experimentally manipulated populations previously at high density and that smaller, less competitive females suffered as a result of the increased competition. The pressure to disperse may therefore be related to the age and social structure of the population. This would explain why populations that experienced high weasel-predation pressure, although similar in density to those in which weasels were absent, appeared to have higher rates of juvenile survival. The effectively 'younger' population, resulting from predation, may have been more permeable to juveniles allowing compensation for the high mortality rate through increased recruitment.

We found no evidence to suggest that weasel predation was sex selective, contrary to the claims of Klemola *et al.* (1997). Klemola *et al.* (1997) found that the mean proportion of pregnant females was lower in control areas than in predator-reduction areas following experimental manipulation, based on an examination of only three or fewer snap-trapped voles, for all but one of their six control sites after the manipulation. As the sex ratio was less male-biased in predator reduction areas, they postulated that small mustelids were selectively preying pregnant female voles, hence magnifying their impact on population growth. However, they lacked the detailed capture-mark-recapture data to substantiate this claim. Our data show that the increase in survival due to reduction in weasel predation pressure was the same for males and females, not greater for females as predicted if weasels selectively predate female voles. In addition, the sex ratio of our vole populations, based on numbers live-trapped, was rarely 1 : 1 during the course of our study. It seems likely that this did not always reflect the actual sex ratio of the population and may simply have been an artefact of method of sampling. For example, if different individuals have different home-range sizes, trappability or activity, their probability of being trapped will vary.

Clearly, if the probability is differential between sexes then it will appear that there is a bias in the sex ratio.

Adult field-vole survival increased in response to suppression of the weasel numerical response in removal sites. It is clear therefore that the effect of weasel removal was not simply negated through compensatory predation by other members of the predator guild in Kielder Forest. Juvenile survival, however, decreased in response to reduction in weasel predation pressure but this reduction in juvenile survival may not have fully compensated for the increase in adult survival in terms of vole population growth. Nevertheless, in spite of the increase in adult survival due to the experimental treatment there was no divergence between control and removal vole populations even during the breeding season when weasel numbers were greatest. In conclusion, the experimental reduction of weasel numbers affected field-vole survival and, although weasel predation can account for a sizeable proportion of the variation in field-vole survival, most of the variation was explained by other factors, probably as a result of the limited seasonal weasel numerical response (Graham 2001). Given that reducing weasel predation pressure had no impact on the size and growth rates of experimentally manipulated field vole populations (Graham 2001), we conclude that changes in weasel predation rate were not responsible for driving the population cycles of field voles observed in Kielder Forest.

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