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Abundance thresholds and the underlying ecological processes: Field voles *Microtus agrestis* in a fragmented landscape

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ABSTRACT

Field voles (*Microtus agrestis*) were trapped in 14 field margins and their behavioural and demographic parameters measured. Strong support was found for thresholds in margin width below which vole abundance was extremely low. Narrow margins were male biased with individuals moving greater distances and a large proportion of males behaved as transient individuals. However, no effect was observed on the age structure or survival of the population. Individuals were able to compensate for the lack of habitat through alterations in their behaviour sufficiently to maintain their survival. Within intensive agro-ecosystems, narrow strips between crops are important links for voles between wider margins and, if available, other more suitable habitats. Maintenance of narrow margins, along with larger areas of suitable habitat, is therefore effective in farmed landscapes for sustaining populations of specialist species where they show sufficient flexibility.

1. Introduction

Habitat destruction and alteration is widespread and well recognised as one of the primary causes of biodiversity loss (Caughley, 1994). Agricultural intensification is one of the main causes of such habitat change and subsequent biodiversity loss globally, due largely to the loss of semi-natural habitat (Benton et al., 2003; Tscharntke et al., 2005; Firbank et al., 2008). Previous research has investigated the effects of habitat loss within agro-ecosystems, primarily on birds (Donald et al., 2001; Vickery et al., 2004) and insects (Rand and Tscharntke, 2007). However, determining how much habitat is required for species persistence, dependent on species site-specific demographic properties, remains a key question in terms of conserving biodiversity both within agro-ecosystems and more generally (Fahrig, 2001, 2003).

Many modelling studies predict the critical size, isolation and configuration of suitable habitat at the landscape scale for population persistence and extinction based on the population dynamics and movement ecology of model species in model landscapes (Lande, 1987; With and Crist, 1995; Bascompte and Solé, 1996; Pearson et al., 1996; Fahrig, 1998, 2001; With and King, 1999). Researchers have commonly reported a non-linear relationship between the occurrence of an organism and the amount of habitat. A critical threshold has been shown to occur below which a small change in the landscape can cause an abrupt change in the probability of population persistence (Fahrig, 1998).

Empirical support for the prediction of threshold responses, although previously sparse, is increasing (Swift and Hannon, 2010). However, not all empirical studies found evidence of threshold relationships between species persistence and amount of habitat (Parker and MacNally, 2002; Lindenmayer et al., 2005). Species with low reproductive rates, high emigration rates and low survival rates in the matrix are most susceptible to changes in their habitat (Fahrig, 2001). Studies associated with threshold responses have generally tested for the presence of a threshold response, precluding inference on the characteristics of organisms likely to experience such thresholds in response to specific properties of the habitat. Consequently, the real value in predicting thresholds is in determining what demographic and behavioural characteristics give rise to the observed thresholds and how these affect the survival of the species, something that existing theory does not deliver as yet.

Within agro-ecosystems, arable fields are largely uninhabitable for many plant and animal species for most of the year, and the grassy strips between them (field margins) are commonly the only remaining areas of semi-natural habitat. These have been shown to be key to the survival of a number of specialist species unable to obtain all their resources (food and protection from predators) within intensely cropped fields (Marshall et al., 2006; Griffiths et al., 2007; Kuykendall and Keller, 2011). Field voles (*Microtus agrestis*) are small mammals that inhabit grassy areas and rely on grass and forbs for food. In intensively farmed landscapes field voles rely pri-

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marily on field margins as habitat (Tattersall et al., 2002). This study is one of the first empirical studies to determine the demographic processes underlying observed thresholds in species abundance in relation to the amount of habitat. This involved determining changes in the population demography (sex ratio, age structure and survival) and behaviour (movement and transience) associated with the observed threshold. It was predicted that a threshold in margin width in relation to vole abundance would occur and margins below this putative threshold width would be used primarily as dispersing corridors. Consequently margins below the threshold would be characterised by: (i) a male biased sex ratio (males are the dominant dispersers (Aars and Ims, 1999)); (ii) a low proportion of juveniles due to a paucity of breeding individuals; (iii) greater individual distance moved by voles (Diffendorfer et al., 1995; Fauske et al., 1997); (iv) higher proportion of transients (animals just passing through the margin); and (v) consequently, lower survival in these margins and in males compared to females due to an increased risk of predation associated with higher mobility along habitat edges and in the matrix (Andreassen and Ims, 1998; Aars et al., 1999; Ims and Andreassen, 2000; Chalfoun et al., 2002).

2. Methods

The study was carried out in a lowland arable agricultural landscape in north east Scotland, approximately 50 km south of Aberdeen (56°8′N, 02°3′W). The area is predominately arable with the remainder grazed by cattle and very little semi natural habitat. Most hedges have been removed and fields are separated by wire fences. Crops grown were primarily cereals (mainly winter sown crops) with a small amount of oil seed rape, root vegetables and daffodils. Field voles were trapped within 14 separate selected margins on seven farms; with two unconnected margins selected from neighbouring fields within each farm. The activity of common weasels *Mustela nivalis vulgaris*, a field vole specialist predator, was assessed on each farm using footprint tunnel tracking (Graham, 2002). Tunnels were placed at approximately 150 m intervals along all the margins within the two neighbouring fields containing the margins used to trap field voles. The number of tunnels per farm ranged from 11 to 21 depending on the size of each field. Each tunnel was checked at two week intervals from the start of May until October, apart from one three week interval in June.

Margins were chosen to border arable fields on both sides (unless one side of the margin bordered a road), be a minimum of 300 m in length and provide a gradient in width ranging from <1 to 14 m. The seven farms were the main arable farms in the area. The average distance between margins on separate farms was 6.3 km (range: 0.2–13.3 km, median: 4.2 km) ensuring independence while maintaining the same topographical characteristics. The distance between the selected margins within each farm was not sufficient to prevent dispersal of voles, however, no individuals were found to move between the margins. All margins 3 m and over were part of an agri-environment scheme and had been planted with a mix of grass seed in 2003.

2.1. Small mammal trapping

Within each margin, voles were trapped along a single 280 m transect of 40 trap stations at 7 m intervals. At each trap station, a minimum of two Longworth traps were used. Prior to trapping, the area was surveyed for signs of vole activity and, in areas where there appeared to be high vole activity (runs and grass clipping), three traps were used at each trap station to avoid trap saturation. Traps were baited with bruised oats, chopped carrot and blowfly (Calliphoridae) larvae, and placed on prebait for two days prior to each trap session. Traps were set in the evening and checked twice daily, in the morning and evening, for five checks. Each site was trapped four times at eight week intervals between April and October 2007. On one farm, one margin was only trapped in April and the other margin only trapped in April and June, due to an unexpected change in farm management. The monitoring of weasel activity was also terminated on this farm in June. Primary sessions are defined as the overall bimonthly trap period per margin and secondary sessions as the individual checks within a primary session.

All field voles trapped were marked with a pair of uniquely numbered ear tags. The mass, sex, and reproductive status of each animal were recorded at the time of first capture in each primary session. Every animal was released at the point of capture. Field voles were classified as adult, young breeder or juvenile based on the following criteria: adults: individuals weighing over 15 g; young breeders: individuals weighing between 10 and 15 g and showing signs of sexual maturity; juveniles: individuals weighing 15 g or less and showing no signs of sexual maturity.

2.2. Statistical analyses

Vole abundance per transect within each primary session was estimated using closed population models implemented in program MARK version 5.1 (White and Burnham, 1999). The capture probability for each trapping occasion and animal was modelled as a function of different combinations of time (t) and behavioural (b) effects and heterogeneity in capture probabilities (h) (White, 2008). The Akaike Information Criteria corrected for small sample size (AICc) (Burnham and Anderson, 2002) was used to select the best fit model. In trap sessions where a low number of individuals were trapped not all model parameters could be estimated. In these margins abundance was taken to be the number of unique individuals trapped (minimum number alive (MNA). Initial data exploration revealed a non-linear relationship between vole abundance and margin width. Tree regressions, implemented in R statistical and programming environment v2.7.2 (R Core Development Team, 2008) using package 'rpart' (v3.1) (Therneau and Atkinson, 2008), were used to establish the existence of potential thresholds in habitat variables in relation to vole abundance. Vole density was estimated by using the area bounded by the total width of the margin multiplied by the transect length plus a buffer of half an inter-trap distance at each end of the transect as the effective trap area.

The sex ratio was calculated as the proportion of females captured within each margin and an index of age structure was calculated as the number of juveniles per adult female captured within each margin per primary session (only a small number of young breeders were recorded, therefore they were grouped together with the adults). The sex ratio and age structure index within each margin was compared to a binomially distributed 50:50 ratio using a binomial test and the effect of margin width was determined using generalised linear mixed models (GLMM) with a binomial error structure and logit link fitted with 'margin' nested in 'farm' as a random factor. One narrow margin with one juvenile present but no adult females was removed from the age structure analysis as it was highly influential. Model assumptions were checked and models were selected using the Akaike Information Criteria (AIC) (Burnham and Anderson, 2002) using the 'lme4' package (Bates et al., 2008). Robustness of model results was checked against the removal of influential observations.

Monthly apparent survival and recapture probabilities of voles were estimated using open population Cormack–Jolly–Seber models with a logit-link function (Lebreton et al., 1992) implemented in program MARK version 5.1 (White and Burnham, 1999). Two analyses were performed: in the first, the data was grouped by margin width (divided into width categories based on output from the