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Meadow voles (*Microtus pennsylvanicus*) in farm landscapes, I. Population parameters in different habitats

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Two microlandscapes were constructed for use in a live trapping study, designed to investigate how meadow vole populations are affected by habitat. Each microlandscape (105 × 35 m) consisted of barley and forage crops (white clover, alfalfa, Canada bluegrass and Kentucy bluegrass), separated by a center plot of undisturbed meadow. Differences in population parameters among habitats were used as indices of habitat suitability. Population parameters were found to differ among habitats; population density, population growth rate, and recruitment showed the greatest variations. Meadow was the highest quality habitat, forage crop was second highest in quality and barley was a low quality habitat. With intensive farming practices, an undisturbed meadow habitat is often rare and highly fragmented. Although forage crops may be common, these habitats are harvested, and are thus only suitable as vole habitats in early summer and late autumn. Persistence of vole populations in farm landscapes hinges on voles not being prevented from disperse among suitable habitats by agricultural crops and tilling practices.

1. Introduction

Human influence, such as agriculture, urbanization and forestry, have fragmented most terrestrial habitats (e.g., Soulé 1986), altered their structure and function, (e.g., Fahrig & Merriam 1994), and threatened the survival of their endemic wildlife (Groombridge 1992). Anthropogenically fragmented areas suffer from habitat loss (Shaffer 1981), reduction in size (den Boer 1981) and increased isolation (Arnold *et al.* 1993). Consequently, efforts to preserve affected species must involve measures to maximize persistence within and among fragment populations (Saunders *et al.* 1991).

Determining the quality, quantity and configuration of all habitats in a fragmented landscape is of fundamental importance for understanding population processes (Pulliam *et al.* 1992). The size and habitat quality of each fragment will determine its potential to sustain a local population (van Apeldoorn *et al.* 1992). Continued survival of each extant populations (Hanski 1991) and recolonization of each habitat patch (Harrison 1991) depends on the species' ability to disperse among habitat fragments with different connectivity (Merriam 1995). Connectivity is a species-specific measure largely determined by the size (Wiens *et al.* 1993), quality (Kozakiewicz 1993), and boundary characteristics (Stamps *et al.* 1987, Wiens 1985) of each habitat, and by the mobility and demands of the species (Hansson 1991).

In most explicit spatial models, high quality habitat dispersion and abundance are considered to be the primary factors influencing regional population. However, the abundance (Andrén 1994) and diversity (Szacki *et al.* 1993) of matrix habitats might be important for the persistence of populations at the landscape scale (Wiens *et al.* 1993). Matrix habitats of high value may also make large contributions to connectivity by serving as 'stepping stones' (*sensu* Ray *et al.* 1991). Despite the obvious need to quantify differences in quality of different habitats at this scale, very little research of this type has been conducted (Hansson 1995, Lidicker 1995). Consequently, very little empirical knowledge exists to describe population dynamics within habitats of different quality.

Agricultural areas are ideal for studying spatial processes. Farming practices, such as cultivating and harvesting, not only increase disturbance frequency (Urban *et al.* 1987) but also increase isolation of natural habitats (Henein & Merriam 1990). Farmers strive to reduce physical and biotic heterogeneity at the patch level, but agriculture, in general, imposes a secondary heterogeneity at the regional level (Merriam 1988). Although the meadow vole (*Microtus pennsylvanicus*) has been observed in farmland, little empirical data exists on habitat preferences and population dynamics in different farmland habitats (Getz 1985).

The objective of this study was to compare the population performance of meadow voles in barley, forage crop and undisturbed meadows. Meadow vole density, individual persistence, population growth, reproductive output, home range size and individual weight gain were the parameters describing population performance in different habitats. Habitats supporting a population with a higher density, more rapid growth, a higher reproductive output and having individuals that persist longer, have smaller home ranges and that gain weight more quickly were considered to offer greater habitat suitablility for meadow voles.

2. Methods

Two rectangular experimental microlandscapes were created and separated by 150 m of old-field successional grassland. An enclosure was constructed around each microlandscape's perimeter with one-meter wide nylon-polyester sheeting fastened to wooden stakes. Twenty-five centimeters of the enclosure wall was buried below ground and curved inward to prevent voles from digging their way out.

Each enclosure measured 105 × 35 meters and was divided into three 35 × 35-meter plots. Center plots were left as undisturbed meadow. Barley was sown in one of the remaining plots (150 kg per hectare of 'Frin' variety spring barley, *Hordeum vulgare*), and a forage crop in the other (10 kg per hectare of 'common #1' white clover, *Trifolium repens*, 10 kg per hectare of 'certified #1 algonquin variety' alfalfa, *Medicago sativa*, 5 kg per hectare of Canada bluegrass, *Poa compressa*, and 5 kg per hectare of Kentucky bluegrass, *Poa pratensis*). In both enclosures, coverage in forage crops steadily increased during the season until a peak in September and early October. In late October, the alfalfa began to wither, quickly being replaced by more white clover and weed species.

Three grids, in a configuration 7 × 7 each, were established in each enclosure with one-meter long wooden stakes marked with coordinates spaced five meters apart. One multiple capture Ugglan live trap was placed within one meter of each grid point. All traps were baited with oats and apple.

Each enclosure was initially emptied of resident voles by four days of continuous trapping. Animals that were released in the enclosures were live-trapped from wild populations in the Gaspereau Valley, Nova Scotia, Canada. These meadow voles were held under standard conditions for five days in captivity at the animal care facility of Acadia University, Wolfville, Nova Scotia, Canada, to suppress their natural homing tendencies. Three randomly chosen females and two males were introduced to the center of each enclosure to establish the study populations. These animals were marked, sexed and examined for their reproductive status (*see* below).

A capture-mark-recapture sampling regime was used in this study. Individuals were marked by toe clipping when first captured, and on all captures weighed and examined for reproductive condition. Males were classified as sexually mature when their testes had descended into a scrotal position. Females with perforated vaginas were deemed sexually active, and those with enlarged nipples and with a noticeable separation between pubic bones, were judged pregnant and/or lactating. All animals were released at their point of capture.

Traps were monitored at 8:30, 13:00 and 18:00, for two consecutive days a week for 20 weeks (13.VI.1994 to 24.X.1994). A five-day period of non-trapping followed each trapping interval, during which traps remained open so animals could enter and leave freely.

In order to prevent the "fence effect", i.e., extremely high densities inside enclosures, sixteen one-way exit tubes were evenly spaced in each enclosure. Exit tubes (77 cm long and 4 cm in diam.) made of ABS piping, were inserted into Ugglan traps located outside the enclosure walls. First time captured individuals were released inside enclosure at their trap point. Second time captives were assumed to be emigrants and were released outside the enclosure. Thus, we hoped that the population dynamics inside the enclosures would more resemble that of a natural population.

All statistical analyses of parametric data were performed with Systat Windows Version 5.03 (Wilkinson 1989). Otherwise, we used tests described in Zar (1984).

Population density was estimated separately for each enclosure. Density estimates were calculated for each trapping day with the Jolly-Seber model (Krebs 1989). Daily population densities in the plots were estimated from the minimum number of different voles caught in a given trapping week, and were compared with a blocked one way Friedman analysis.

Persistence, or the probability of an individual remaining in the trapped population, was estimated from the number of days that each vole was known to be within the study plots. Estimates were calculated only for individuals that limited all of their activity to a single plot.

The finite rate of increase lambda (λ), was calculated (as the population size at t +1 over the size at t) (Caughley 1977) between weekly trapping sessions for each plot type.

We used recruitment as an index of female reproductive output. It was calculated as the proportion of individuals that were juvenile first captures, caught in a given trapping session.

A home range size was determined with an index calculated as the number of different traps each vole was caught in, multiplied by the area surrounding each trapping station (25 m^2).

We used an individual weight gain as an index of habitat quality for different plot types. The weight gain (grams per day) was determined by dividing weight at $t + 1$ by weight at t. Only voles that confined all their activity to a single plot, and were caught in at least two weekly trapping sessions were used.

3. Results

A total of 243 individuals were trapped 1 857 times in this study, of which 1 241 were in enclosure E1 and 616 in enclosure E2. Trappability was generally high but differed between E1 (93% ± 5%) and E2 (85% ± 12%) ($n = 18$, $t = 2.069$, $p = 0.011$).

Population densities were similar in both enclosures until early September when the populations in E1 increased exponentially to a peak density, two weeks before the end of trapping. The abundance of voles in E1 was more than three times higher than the maximum density reached in E2.

Daily densities (number of individuals), within each enclosure, were almost always the highest in the meadow (13.98 ± 9.99), intermediate in the forage (6.55 ± 9.69), and consistently lowest in the barley (1.25 ± 1.33) plots (Fig. 1). A one way blocked design Friedman analysis ($\chi^2 = 62.3$, $p < 0.0001$, df = 2) revealed statistical differences among all the plots.

Persistence was calculated for voles limiting all their activity to a single plot. Female (27.5 ± 16.6, $n = 104$) and male (19.0 ± 8.2, $n = 84$) persistence values did not differ significantly ($t = 2.056$, $p = 0.065$), and thus, they were pooled for interplot comparisons. Mean persistence did not differ (Friedman $\chi^2 = 1.0$, $p = 0.61$, df = 2) among the meadow (15.6 ± 23.3), forage (10.9 ± 12.4) and barley (13.7 ± 24.4) plots.

The finite rate of population increase (λ), was on average the highest in the meadow (1.19 ± 0.53), intermediate in the forage (0.84 ± 0.86) and the lowest in the barley (0.7 ± 0.89) plots. A one way Friedman test revealed a relatively strong plot effect ($\chi^2 = 6.09$, $p = 0.05$, df = 2). However, post hoc comparisons indicated interplot growth differences only between the meadow and barley areas (Tukey test, $q = 4.08$, $0.025 > p > 0.01$, df = ∞).

Reproductive output was determined from the number of juvenile first captures found in each plot type. More recruits were caught in E1 than E2; within each enclosure most juveniles were caught in the meadow (54 recruits), followed by the forage (40 recruits) and then the barley (2 recruits) plots. Mean daily recruitment rates (within plots) were similarly high for the meadow (0.046 ± 0.084) and forage areas (0.045 ± 0.088), but much lower for the barley ones (0.008 ± 0.053). Recruitment rate varied among plot types ($\chi^2 = 7.96$, $p = 0.019$, df = 2), post hoc comparisons revealed large differences among the meadow and barley areas ($q = 4.902$, $0.005 > p > 0.001$, df = ∞).

The home range sizes of adult females, confining their activity to a single plot were estimated.

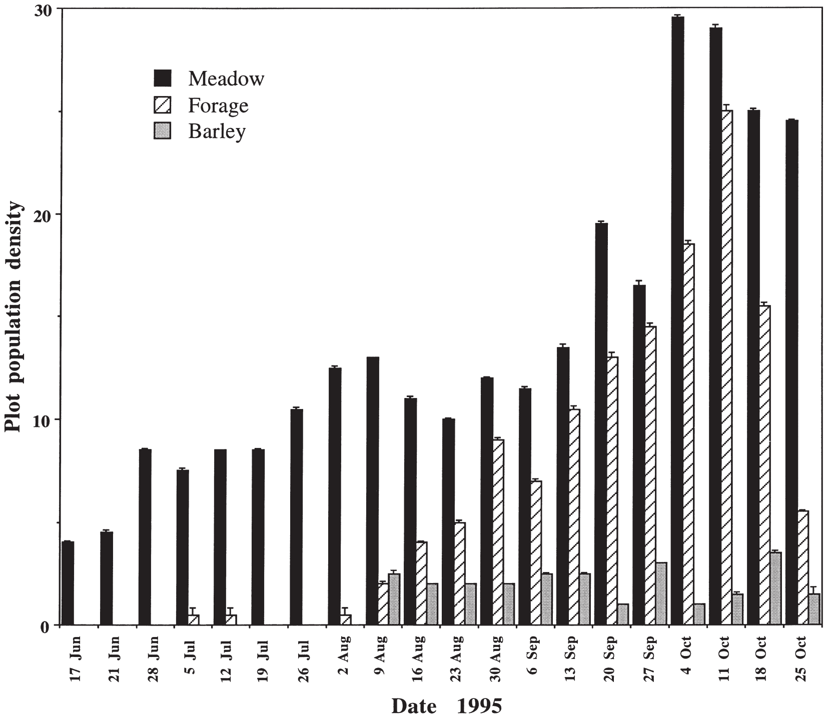

Fig. 1. Direct enumeration estimates for plot population density, based on the number of individuals caught at least once in each given week of trapping. Estimates have been averaged (± standard error) between enclosures.

As only one vole restricted its activity to the barley plot, this plot was excluded from the analysis. A Wilcoxon paired sample test did not reveal differences in the home range sizes in the forage (146.15 ± 61.95 m^2, $n = 13$) and meadow (196.59 ± 135.69 m^2, $n = 22$) plots (Wilcoxon test statistic = 1.683, $p = 0.092$).

A juvenile weight gain (g day^{-1}) did not differ between individuals in the forage (0.91 ± 0.56, $n = 13$) and meadow (0.74 ± 0.55, $n = 32$) areas (Wilcoxon test statistic = 1.18, $p = 0.248$). The low sample size prevented inclusion of individuals from the barley plot in the interplot comparison of weight gain.

4. Discussion

It is generally assumed that site suitability for a given species should be measured in terms of its potential to maintain a persistent population, where greater population density is interpreted to reflect a higher quality habitat (Schamberger & O'Neil 1986). However, several authors (Van Horne 1983, Pulliam 1988, Hobbs & Hanley 1990, Howe *et al.* 1991) showed the importance of considering habitat suitability or quality more explicitly, in terms of individual survival and fecundity. As a consequence, several population parameters were included in this study as indices of habitat quality.

Although the enclosures were chosen as replicates, the populations within each differed; in the autumn, the population in E1 increased threefold as compared to the one in E2, and more recruits were caught in E1 as compared with E2. Enclosure E2 was on a slightly higher ground than E1 and thus dried. This may have caused the difference in population attributes between enclosures. However, these differences were accounted for in the analyses.

Several population parameters were shown to vary among the experimental plots, providing some evidence of spatial substructuring at this scale (Table 1). The meadow vole populations in the barley plots showed the lowest densities, individual growth rates and recruitment levels. The forage crop plots supported fewer animals than the meadows, but populations within these plot types exhibited similar growth rates and recruitment levels, individual persistence, home range sizes and individual weight gains. The results indicate meadows as the most suitable habitat for supporting viable meadow vole populations, forage habitats were intermediate, but these habitats are often harvested or grazed by livestock. Barley could be classified as an unsuitable habitat for meadow voles.

Density differences among habitat types are common in *Microtus* populations (e.g., Foster & Gaines 1991, van Apeldoorn *et al.* 1992).

Microtus spp. survival has been shown to be positively correlated with resource availability; animals in high quality habitats are more likely to live longer and less likely to leave (Ostefeld *et al.* 1985, Adler & Wilson 1989, Foster & Gaines 1991, Hall *et al.* 1991). Persistence rates were compared between sexes because male *Microtus* tend to emigrate more often than females (Gaines *et al.* 1979, Madison 1980, Baird & Birney 1982, Johnson & Gaines 1985, Ims 1987). In our study, persistence levels did not differ significantly between sexes which also indicates that the enclosures had capacity to contain vole populations. Our results did not support previous predictions that persistence rates should be lower in less densely covered areas (Ostefeld *et al.* 1985, Adler & Wilson 1989, Foster & Gaines 1991, Hall *et al.* 1991).

Rate of increase (λ) was included as an index of population 'health', giving an average measure of effects of environmental stress on several population parameters (Caughley 1977). This measure could be considered as an alternative to the traditional density estimate (*see* Van Horne 1983), which has been shown, by modeling, to be inaccurate for predicting a habitat's carrying capacity (Fahrig & Paloheimo 1988, Hobbs & Hanley 1990). Lambda has also been applied in a minimum viable population analysis (e.g., Menges 1990), serving as a general measure of viability. The meadow area was the only habitat which sustained viable populations (average $\lambda > 1$), *see* Menges 1990. Post hoc comparisons revealed interplot differences only between the barley and meadow habitats. This means that, despite having a lower overall density, the resident forage crop population was responding similarly to its habitat as the local meadow population.

Habitat differences in overall recruitment can be a function of density, but variations in recruitment rate usually reflect habitat differences (Bondrup-Nielsen 1986). *Microtus* reproductive performance has been shown to be closely influenced by food quality (Batzli 1983) and cover (Ostefeld *et al.* 1985, Hall *et al.* 1991). Here the voles' recruitment rates were shown to differ only between the barley and meadow areas. This again indicates that forage vegetation offers comparable benefits to meadows.

A home range size has been shown to be negatively associated with the population density (Bondrup-Nielsen 1986, Gaines & Johnson 1982) and resource abundance (Jones 1990). Many authors discuss an appropriate method for measuring a home range size (e.g., Metzgar & Sheldon 1974, Madison 1985, Bondrup-Nielsen 1986); however, each method produces at best only an index (Bondrup-Nielsen 1985). Since male voles tend to wander more extensively than females (Madison 1980, Ims 1987), and juveniles tend to aggregate around their natal area (Myllymäki 1977), they were excluded from the home range estimates. The home range size of reproductive females did not differ among the plot types, i.e. the density related to the home range size. It was determined only for individuals that confined all of

Table 1. Comparison of population parameters among the meadow, forage and barley plots (Lambda = finite rate of increase).

Parameter	Meadow	Forage	Barley
Population density	High	Medium	Low
Persistence	Same	Same	Same
Lambda	High	Medium	Low
Recruitment	High	Medium	Low
Home range size of			
reproductive females	Same	Same	NA
juvenile weight gain	Same	Same	NA

their activity to a single plot; most of these coming from E1 during the autumn months when the voles' densities in the forage and meadow plots were very similar. This may indicate that the habitat quality was the only factor affecting the home range size; female voles in each of the two habitats were able to fulfill all their life history needs within similar sized areas in different habitats. Similarly, the weight gain did not differ between the forage and meadow plots. The two areas, thus, appear to provide equal quality dietary choices for young voles.

The barley and forage crops seemed to serve as barrier habitats (*sensu* Anderson 1980) until offering more coverage in August. The voles in the forage plots exhibited similar densities, population growth, recruitment levels, home range sizes and individual weight gains as in the meadow habitat. Further studies are needed, however, to establish the forage crop's long term capacity for maintaining population viability without immigration from adjacent meadow habitats (*see* Van Horne 1983). Assuming the rescue effect (Brown & Kodric-Brown 1977) is operating here, this type of habitat still has the potential to influence metapopulation dynamics (Pulliam 1988) and/or serve as a stepping stone (Ray *et al.* 1991).

The barley plot was usually frequented for short periods of time, and these visitors made a large contribution to the estimates in barley plots. Although the crop did provide significant cover by the end of the season (weeds and all), its lower food quality and dryer conditions may have prevented colonization by the mesophilic meadow vole (Getz 1985). The barley cover also seemed to be more affected by rain and wind, bare ground was often temporarily exposed. This habitat did not appear to provide the resources necessary to support viable meadow vole populations; by far, most voles used it for transit only (gestational females were never seen). Barley fields (and likely other grain fields) will make relatively small contributions to regional population survival.

An undisturbed old meadow habitat is essential for the persistence of meadow vole populations in farmland. Although forage crops did provide a suitable habitat for voles these crops are harvested or animals forage on them, thus rendering them suitable only when left undisturbed with good coverage. The essence of the persistence of meadow voles lies in the connectivity of fields surrounding old field meadow (Basquill and Bondrup-Nielsen 1999). If old field meadows are too isolated or the connectivity to the surrounding fields are poor, meadow vole populations may locally go extinct.

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