

## Reproductive asynchrony and its potential role in the mating system of meadow voles

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Ims (1987a) hypothesized that the spatial distribution pattern of male voles may be influenced by the temporal distribution of females. When females enter estrus synchronously (i.e. are clumped in time) they represent a defendable resource and males should defend a territory containing a cluster of females. When females breed asynchronously, males should not be territorial. In this study we examined the role of female breeding synchrony on the spacing strategies of male meadow voles *Microtus pennsylvanicus* (Ord, 1815). Maternity was determined by the transfer of a unique combination of radionuclides from mother to offspring. The date of conception (to the nearest week) was determined by the weight at first capture of newly recruited voles. The number of litters conceived per week ranged from zero to four. The null hypothesis that the number of litters conceived per week was distributed randomly could not be rejected in 8 of 9 grid-years (4 years on 3 grids). This finding of breeding asynchrony in a vole species with nonterritorial males is consistent with Ims' hypothesis.

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### Introduction

Despite a rich history of theories linking social behavior to population dynamics of voles and lemmings (Taitt and Krebs 1985, Heske *et al.* 1988), hypotheses concerning the ecological causes of social organization are relatively new. Ostfeld (1985) proposed that the spatial distribution of breeding females (territorial or nonterritorial) was determined by the distribution and renewal rates of food resources. The spatial patterning of females, in turn, determines whether or not conspecific males defend territories. According to Ostfeld (1985), when breeding females are clumped in space, they constitute a defendable resources for males, who should then defend territories containing clusters of females. When females are uniformly distributed due to their territorial behavior, males should move among female territories rather than defend a territory of their own.

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Ims (1987a) extended this hypothesis to include the availability of females over time. According to Ims (1987a), when females enter estrus synchronously, they constitute a monopolizable resource and males should be territorial. When synchronous females have home ranges that are small and/or are clumped in space (i.e. nonterritorial) more than one female can be defended and the mating system should be polygamous. When synchronous females occupy large and/or widely dispersed home ranges (territorial) only one female can be economically defended and the mating system should be monogamous. When females breed asynchronously, whether or not they are territorial, they are not a defensible resource and males should not be territorial, but instead must wander among female territories to assure their reproductive success.

Little information is available to test Ims' (1987a) hypothesis. Ims (1988) showed that the spatial distribution of female grey-sided voles *Clethrionomys rufocanus* is resource dependent whereas the spatial distribution of males depends on the distribution of mates. However, due to the paucity of field data on breeding synchrony in voles, it has not been possible to assess the relative importance of spatial and temporal distributions of receptive females in determining the behavioral strategies of males. Conventional livetrapping techniques offer insufficient resolution of the timing of breeding events. Kill-trapping studies are better for assessing reproductive synchrony, but are disruptive to social organization.

Herein we use data from a field study of meadow voles *Microtus pennsylvanicus* (Ord, 1815), to address the role of breeding synchrony of females in spacing strategies of males. Specifically, we determined the degree of reproductive synchrony of female meadow voles, a species in which males are known to be nonterritorial (Madison 1980, Webster and Brooks 1981, Ostfeld *et al.* 1988). According to Ims (1987a) female reproductive asynchrony is a necessary characteristic of populations with nonterritorial males. The finding that reproduction is synchronous would refute Ims' (1987a) hypothesis for meadow voles.

## Methods

### Study area and trapping

This study was conducted on three 0.7-ha grids in South Natick, Massachusetts, USA, that have been the site of long-term studies of meadow vole population ecology (Tamarin *et al.* 1984, Ostfeld *et al.* 1988, Pugh and Tamarin 1988, 1990, 1991). Two of the grids (K and L) were surrounded on all sides by a vole-proof fence made of corrugated metal. A 0.2-ha area of woodland was included within each fenced grid to create a dispersal area or sink (Lidicker 1975). Tamarin *et al.* (1984) showed that with this design, normal demographic processes occurred within the enclosed populations. The third grid (M) was open on three sides and served as a control. After all individuals were removed from each grid by trapping, 13 to 15 adult and subadult ( $\geq 22$  g) voles were released on each grid in July, 1985 in combinations to maximize electrophoretic heterozygosity.

One hundred Ketch-all, multiple-capture live traps were baited with oats, supplied with cotton bedding, and set in each area in a grid pattern with 7.6 m between trap stations. Except for midwinter nonbreeding periods, trapping was conducted biweekly from August 1985 to December 1988. Traps



were set late in the afternoon on the first day of each trapping period and checked on the following two mornings. Upon capture each vole was given an individually numbered ear tag and data on reproductive condition (males: testes abdominal or scrotal; females: vagina nonperforate or perforate; lactation tissue small, medium, or large; and pubic symphysis closed, slightly open, or open), location, and weight were recorded. All animals were removed to a nearby field site for further processing and returned to their capture location within 3 hr. Six pitfall and 21 Ketch-all traps were set continuously in each dispersal sink during the 1986 trapping season only and checked at 2- to 3-day intervals. All voles captured in the dispersal sinks were removed permanently.

#### Determination of reproductive synchrony

Conventional trapping data (individual identity, location, weight, and reproductive condition) do not provide sufficient information to accurately estimate dates of parturition and conception. However, if mother-offspring relationships are known trapping data from both mothers and offspring can be used to estimate these dates with a resolution of one week or less. To this end we determined patterns of relatedness and reproductive success by a radionuclide technique (Tamarin *et al.* 1983, Sheridan and Tamarin 1986, 1988, Ostfeld *et al.* 1988, Pugh and Tamarin 1988, 1990, 1991). Briefly, it involved injecting all captured females that were either lactating or pregnant (determined by palpation) with a unique combination of two gamma-emitting radionuclides. Trappability was high, averaging 87% over the course of the study. We are confident that all females were injected during the course of their pregnancy or period of lactation. Maternity was determined by the transfer of radionuclides from mother to offspring via the placenta or through milk. Upon initial capture all voles were checked for radionuclide burden with a portable whole-body counter. The presence of isotopes in a new recruit was used to identify its mother. The approximate date of birth and date of conception (assuming a 21-day gestation) of a litter was estimated to within 1 week based on the trapping records of the mother and offspring, the weight at first capture of the recruits, and growth curves of young voles in laboratory colonies (Morrison *et al.* 1977, Innes and Millar 1979) as well as from our own field data. Age determination is less accurate for older recruits with a high weight at first capture. Therefore, only litters with individuals whose weight at first capture was  $\leq 20$  g were included in the analysis.

The numbers of litters conceived per week from which individuals were subsequently recruited into the population were determined separately on each grid for the years 1985–1988. Since meadow voles typically have a 21-day gestation period with a postpartum estrus (Keller 1985), each breeding season was divided into a series of 3-week blocks beginning with the week of the first conception. The number of litters conceived in each of the 3 weeks of each block were summed over the entire breeding season. An index of randomness ( $s^2 / \bar{x}$ ) was calculated for each grid in each year to estimate the degree of breeding synchrony within the populations (Kawata 1985, McShea 1989, Sikorski and Wójcik 1990). An index value of 1 indicates breeding occurs randomly in time. An index value significantly  $> 1$  indicates synchronous breeding, and a value significantly  $< 1$  indicates a uniform breeding pattern. Significance was determined by a  $X^2$  analysis (Southwood 1978). This index is especially useful when evaluating the distribution of a rare event in space or time (Sokal and Rohlf 1981). Our finding that individual males typically range over at least 20% of a grid (Ostfeld *et al.* 1988) indicated that the grid was an appropriate scale over which to assess the determinants of male mating strategies.

### Results

The density of voles on all three grids was low to moderate over the 4 years of the study (Fig. 1 in Pugh and Tamarin 1990). The highest densities (93 voles/ha) occurred in 1986 and the lowest densities ( $< 10$  voles/ha) occurred in early 1987

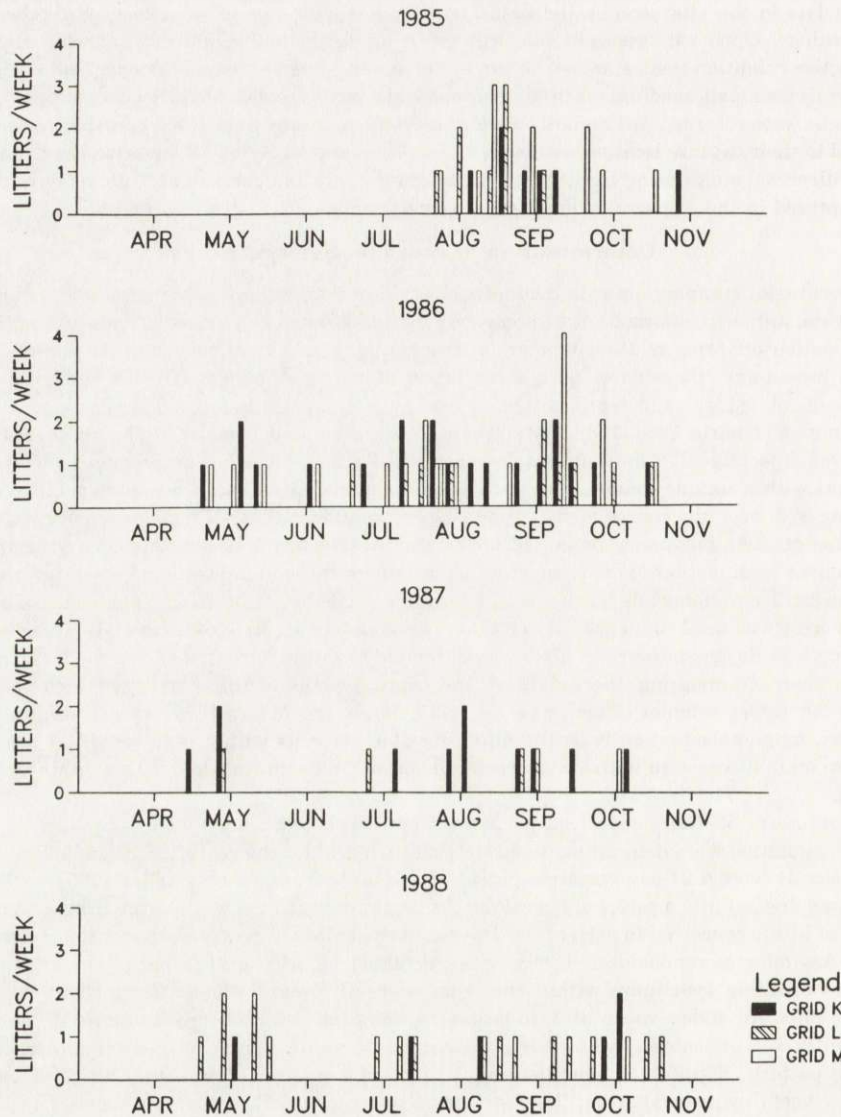


Fig. 1. Frequency distribution of the number of meadow vole litters conceived per week that were recruited into the population in South Natick, Massachusetts. Trapping began in August 1985 and terminated in December 1988.

and 1988. Although some variation in density did occur between years, these populations did not appear to undergo the 3 – 5 year multiannual fluctuations in density typically reported for this species. The number of reproductive females per grid per breeding season averaged 19.6 (SD = 13.5) and ranged from a low of 8 on grid K in 1985 to a high of 51 on grid M in 1986.



Table 1.  $X^2$  analysis of the index of randomness ( $s^2/\bar{x}$ ) of breeding synchrony in meadow voles on three grids (K, L, M) in Massachusetts, USA. The null hypothesis that litters are distributed randomly through time will be rejected when  $p < 0.05$  (clumped) or  $p > 0.95$  (uniform, Southwood 1978).

Grid	1985			1986			1987	1988	
	K	L	M	K	L	M	K	K	L
$s^2/\bar{x}$	0.57	2.37	1.00	0.05	0.63	0.06	0.37	0.50	0.41
$X^2$	1.14	4.74	2.00	0.10	1.26	0.12	0.74	1.00	0.82
$p$	> 0.25	> 0.05	> 0.10	> 0.95	> 0.25	> 0.90	> 0.50	> 0.50	> 0.50

The mean number of litters successfully recruited per breeding season per grid was  $9.2 \pm 6.1$  (mean  $\pm$  SD, range 1 – 20). Only one litter was recruited on grid M in 1987 and 1988 and only four litters were recruited on grid L in 1987. A test of the null hypothesis of random timing of litters was not possible in these cases. Eliminating them left a sample size of nine grid-years.

The number of litters conceived per week from which individuals were subsequently recruited into the population ranged from zero to four (Fig. 1). During all breeding seasons and on all but one grid, the null hypothesis that breeding events were distributed randomly through time could not be rejected (Table 1). On grid K breeding events were actually distributed uniformly in time during the 1986 season. We conclude that the voles in these populations were not breeding synchronously.

### Discussion

Ims (1987a) predicted that asynchronous breeding among female voles should cause males to adopt a nonterritorial, mobile strategy of space use due to the inability of individual males to monopolize multiple mates (Emlen and Oring 1977). The meadow voles we studied bred asynchronously, which is consistent with Ims' (1987a) hypothesis because male meadow voles are nonterritorial (Madison 1980, Webster and Brooks 1981, Boonstra and Rodd 1983). Indeed, a radiotelemetry study performed on this population during the course of the current study on one of the trapping grids (grid M) revealed that the home ranges of males overlapped extensively (Ostfeld *et al.* 1988). The temporal availability of mates may therefore play a role in the adoption of space-use strategies by male voles.

Ims (1987a) also suggested that reproductive synchrony is maintained by frequent contacts among neighboring females, which may entrain estrous cycles. Since our population remained at low to moderate density, the potential for frequent contacts was relatively low. Therefore, it is possible that at higher densities female meadow voles may breed more synchronously than we found. If so, territoriality in males would be expected. However, we are not aware of any studies

demonstrating territoriality in male meadow voles, irrespective of population density. Female meadow voles have been shown to be territorial during the breeding season at all densities studied (Madison 1980, Webster and Brooks 1981, Ostfeld *et al.* 1988). However, increasing density can also affect other components of vole social systems such as the number of males or females in reproductive condition, home range size and overlap, and individual spatial distribution patterns (Bujalska and Grüm 1989).

Before we can evaluate the significance of our results, two potential weaknesses in our analysis must be addressed. First, whereas Ims' (1987a) hypothesis concerns the temporal distribution of estrous females, we measured the timing of only those estrous events that led to successful recruitment of offspring into the population. Elimination of estrous events that did not result in conception nor produce surviving offspring reduces sample sizes, but should not introduce any systematic bias. Thus, synchrony of estrus should be reflected in synchrony of recruitment. Moreover, estrous events that do not produce surviving offspring should have only a minimal impact on the evolution of spacing strategies since these unsuccessful matings do not increase fitness. Whereas males may not be able to differentiate between successful and unsuccessful matings, only those matings that ultimately produce surviving offspring can have an impact on the selection of mating strategies by males. Therefore, we feel we have addressed a meaningful aspect of the temporal availability of mates.

Second, our technique permitted a resolution of conceptions only to a level of a week. This could cause a systematic bias towards finding synchrony since all breeding events scattered over one week are assigned to a single block; populations that breed asynchronously at a level of resolution of less than one week could be labelled synchronous using our technique. Our finding of asynchronous breeding is therefore conservative. In addition, 1-week periods may in fact be appropriate time intervals with which to measure breeding synchrony. To our knowledge the precise degree of breeding synchrony necessary to allow individual voles to defend multiple mates has not been determined. Ims (1987a) suggested that perfect synchrony was not necessary to promote territoriality in males. Indeed, extreme synchrony (e.g. all females entering estrus in the same hour) would certainly not promote territoriality by males due to the time required for courtship and copulation. While a male is courting and mating with one female, other females who come into estrus simultaneously are available for pursuit by rival males. This range of synchrony falls within the framework of territoriality models that describe two thresholds, one at each end of the resource availability axis, that define defendability (Brown 1964). We suggest that a moderate degree of synchrony of estrous events within the range of several days to a week would facilitate male territoriality, whereas asynchrony at the level of one week, such as we found, would discourage it.

McShea (1989) found that adjacent pairs of female meadow voles tend not to breed synchronously. He reported that females appear to adjust the timing of



reproduction to be out of phase with their neighbors, causing reproduction to be temporally overdispersed. However, he did not eliminate the possibility of a temporally random distribution of breeding events. Moreover, since breeding female meadow voles tend to have a uniform distribution in space (Madison 1980, Ostfeld *et al.* 1988), it should not be possible for each female to be out of phase with all neighbors simultaneously. At the level of the local population, it seems likely that breeding events in the voles McShea (1989) studied were spaced randomly in time. In any event, we show a lack of reproductive synchrony in meadow voles at a moderate spatial scale that had been previously demonstrated at a small spatial scale (McShea 1989).

Ims (1987b) reported an asynchronous onset of breeding in the grey-sided vole *Clethrionomys rufocanus*. Because synchronous breeding throughout the reproductive period requires a synchronous onset of breeding (Ims 1987a), it is likely that breeding for this population was asynchronous for the entire season. Since this species is known to have territorial females and nonterritorial males (Bondrup-Nielson and Karlsson 1985), these results are similar to ours. Asynchronous onset of breeding has also been reported for other species of *Clethrionomys* (Ims 1987a, Bujalska 1990). In contrast, Sikorski and Wójcik (1990) documented reproductive synchrony in an overwintering population of bank voles *C. glareolus*, a species with territorial females and nonterritorial males. This finding refutes Ims (1987a) prediction. He would have predicted male territoriality in this population. Kawata (1985) described a spring population of red-backed voles *C. rufocanus* that bred synchronously. As in the above populations the females in this population defended territories whereas males were not territorial. However, Kawata's (1985) study also included only overwintering females early in the breeding season, and it is possible that synchrony degenerates later in the season. Nevertheless, litters born synchronously to pairs of females with adjacent home ranges were sired by different males (Kawata 1985), indicating that in this species synchronous breeding does not necessarily enhance the ability of males to monopolize mates (Ostfeld 1990). Overwintering female wood lemmings *Myopus schisticolor*, were also found to breed synchronously (Ims *et al.* 1988). Ims *et al.* (1988) had frequent captures of more than one adult female at a trap station indicating that females may have had overlapping home ranges. Unfortunately the degree of overlap of home ranges of males is not known. Ims (1987) would predict territoriality among male wood lemmings.

There are two other situations in which Ims' (1987a) hypothesis should be tested. First, *Microtus californicus* has nonterritorial females and territorial males (Ostfeld 1986). Ims (1987a) would predict that breeding would be synchronous. Unfortunately we are not aware of any data on breeding synchrony in *M. californicus*. Second, an experimental situation could be created in which a species that normally demonstrates female territoriality and breeding asynchrony (e.g. *M. pennsylvanicus*) is artificially synchronized by endocrine stimulation. If males became territorial then Ims' (1987a) hypothesis would be more strongly supported.



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