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Vole Population Cycles: A Case for Kin-Selection?

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Summary. Kin-selection, as evidenced by aggression between individuals with a low coefficient of relation, may be a significant contributing factor in vole population cycles. Demographic and behavioral studies support this idea.

Population biologists have for many years been interested in the regular fluctuations in numbers exhibited by many microtine rodents (Chitty, 1967; Krebs et al., 1973; Krebs and Myers, 1974; Tamarin, 1978). Chitty (1957, 1960) proposed that population increase might be tempered by deterioration in the quality of the population as a result of selection on genetically determined behavioral types. More specifically he suggested (Chitty, 1967) that the genetic composition (of the population) changes during the cycle – that selection favors large, aggressive animals with low reproductive rates at high densities, and smaller, less aggressive animals with high reproductive rates at low densities. Thus spacing behavior, measured as aggression, would drive the demographic machinery through the cycle. Much recent work has focused on genetic changes (natural selection acting on individual advantage) during the population cycle (e.g., Krebs and Myers, 1974) and has demonstrated the possibility of selection operating on this time scale (although evidence is still only preliminary and suggestive). An additional factor has been implicated as an important contributor in these cycles: dispersal (Krebs et al., 1973; Pitelka, 1973; Krebs and Myers, 1974; Tamarin, 1978).

We wish to suggest an alternative type of genetic change which may play some role in the cycle. Consider a population of voles at a low point in the cycle. As the population begins to build, dispersal by individuals from their natal areas becomes an important part of the population dynamics. Dispersal remains high until the population declines. Studies of *Microtus pennsylvanicus* in southern Indiana suggest that if dispersal is prevented in an oscillating population accustomed to dispersal, the population density may not be regulated at a level below that of gross starvation (Krebs et al., 1969); studies of *Microtus breweri* on an island off the coast of Cape Cod suggest that if dispersal is not possible over a long time span, cycles may not occur (Tamarin, 1978).

At a population low (with little dispersal) individuals interact with others in their neighborhood, and these are probably close relatives (Hamilton, 1964, 1971, 1972). The coefficient of relationship, which mediates the degree of altruism and selfish behavior among individuals, is on average high between individuals in a neighborhood. However, the situation rapidly changes as the population increases and dispersal becomes important. Migrant individuals entering a neighborhood are probably unrelated to the residents. With high dispersal the average coefficient of relationship between individuals in a neighborhood *rapidly* drops. Along with this drop is predicted an increase in aggression between individuals. Note that the genetic change is in the relatedness of individuals in a given geographic location; it is brought about simply by the dispersal itself, and does not require that the dispersers be of a different genotype than those who remain at home (Myers and Krebs, 1971). Interestingly, this model predicts that aggression should remain elevated as long as the coefficient of relationship is low. This will be true as long as dispersal is high. As dispersal decreases there should be a gradual increase in numbers of relatives in one's immediate neighborhood; aggression should drop and a population increase should begin.

Is this proposition supportable on the basis of what is now known about cycles in vole populations? It has become increasingly clear that the general pattern for cyclic microtines is to persist mainly on restricted "islands" of favorable habitat during years of population lows, and then to disperse into less favorable habitats as numbers begin to increase. This type of patchy distribution is important for the proposed model, and implies that non-cycling microtine populations may inhabit more continuous environments. The major importance of dispersal has recently been accentuated by studies on lemming populations at Barrow, Alaska: brown lemmings were quite scarce through the summer of 1970 yet in June 1971, with overwinter vegetation in good condition, winter nests scarce, young brown lemmings rare and little incidence of reproduction in females (all atypical of population peaks), brown lemmings reached numbers as high as in the best years. "All these facts in combination indicate that the bulk of the brown lemmings present near Barrow in June had 'immigrated'" (Pitelka, 1973).

Working in Manitoba, Turner and Iverson (1973) found that aggressive behavior in male *Microtus* increases during the breeding seasons, and is enhanced by decreasing size of home range. As local populations gradually increase, this aggressive behavior could initiate dispersal. Once dispersal begins it could be accelerated by the rapidly dropping average coefficient of relationship between individuals, leading to increased aggressive behavior; several studies suggest that animals in peak populations are in fact the most aggressive (see review in Krebs and Myers, 1974). While Turner and Iverson (1973), looking at annual population changes, could not find a consistent relationship between aggressive levels and population density, they did find dominant voles to be usually heavier; and increased body size in peak populations is one of the generalized features of long-term rodent population cycles (Chitty, 1952; Krebs and Myers, 1974). How this size change might be directly related to the proposed model is not yet clear.

Dispersal probably stops simply due to saturation of the local environment. The extent of this saturation would depend on the carrying capacity, which could vary from cycle to cycle due to changes in quantities of nutritious forage, extent of favorable habitats, etc. This could account for the observation that "high population density is not sufficient to produce a decline, and low density is not sufficient to stop a decline" (Krebs and Myers, 1974); clearly the concept of density may not just be related to numbers per unit area, but would likely also include numbers relative to available food supplies. Saturation would mean that the environment had been pushed to its limits, but not necessarily that it had been completely depleted by overgrazing. Saturation might also explain the possibility that losses by emigration may be proportionally highest in the increase phase and lowest in the decline phase (Myers and Krebs, 1971).

Once dispersal has ceased, a period of time will need to pass to restore relatedness in local populations. During this period behavioral interactions may affect reproduction and growth: this has been demonstrated in confined populations (Christian, 1971), but not yet in field populations. Social intolerances may also stress "minority" individuals and make them more susceptible to loss by predation, extreme weather or disease (Krebs and Myers, 1974). These responses may provide the steady mortality factor of small magnitude (a 10–15% drop in the probability of survival per month is sufficient for most declines) which can account for most losses in declining populations (Krebs and Myers, 1974). These declines would be attributable to intraspecific aggression; thus one would not be surprised to observe that *M. ochrogaster* suffered high mortality and numerical decline at a time when *M. pennsylvanicus* was surviving successfully in the same Indiana field (Krebs et al., 1969); or that an increased population of *Lemmus lemmus* in Finland occurred simultaneously with a decreased population of *Microtus agrestis* (Tast and Kalela, 1971). As populations decline they should quickly withdraw from unfavorable habitats, re-establishing local "islands" with an increasing average coefficient of relationship. Thus the stage would be set for another cycle.

The best test of this hypothesis would be to measure the average coefficient of relationship of individuals close to each other (i.e., adjacent traps) during population lows and highs to see if these are in any way correlated with behavioral observations. The relatedness might be estimated on the basis of gene frequency using electrophoretic techniques. The experiments of Smith et al. (1975) and Garten (1976) offer an example of how these experiments might be approached, and their observation of a correlation between the percent of heterozygosity and the ability to compete aggressively in a population of oldfield mice suggests that relatedness of individuals, which might be inversely proportional to heterozygosity, could be a significant driving force in population cycles.

Since our hypothesis suggests that changes in social structure should accompany changes in population density, it would be useful to know directly if such changes occur. For instance: does the mating system alter due to the movement of foreign males into or through an area. Such data are not at present available.

Hamilton (1971, page 77) independently proposed that the general level of aggressiveness in a population will increase during periods of high dispersal (and will remain raised until a higher average relationship between neighbors has been re-established). It would probably be naive, in view of what is known about vole cycles, to suggest that any single factor is the sole driving force for these oscillations (consider Finerty, 1980); what we propose is that since the "genetic change" (population structure) requires *only* dispersal, and since it will be reversed when (perhaps only when) dispersal is curtailed and population density decreases, this change could be a contributing factor driving population cycles.

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