

Barriers as boundaries for metapopulations and demes of *Peromyscus leucopus* in farm landscapes

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Abstract

Effects of potential barriers (roads and cultivated fields) on both demographic and genetic features of subpopulations of white-footed mice were studied near Ottawa, Canada. Live trapping, colored bait and track registry were used to study animal movements across roads on four 1.44 ha areas each within a small forest bisected by a narrow gravel road. The genetic study was done in 11 other forest fragments separated from each other by cultivated fields. Frequencies of three electrophoretic variants of salivary amylases were established for mice caught in each patch of wood and genetic similarity of subpopulations was calculated. Movements of mice across the roads were very infrequent (quantitative barrier), although movements adjacent to roads were frequent and long enough to cross the roads. Salivary amylase data showed that studied subpopulations were genetically very similar although the sample was intentionally biased toward demographic isolation. Results are discussed in terms of possible hierarchical relationships of metapopulations and genetic demes in the context of landscape ecology, management and conservation practice.

Introduction

Much recent research supports the concept that many animal populations in heterogeneous environments are structured, spatially and functionally, as demographic metapopulations in the sense of Levins, 1970 (Pickett and Thompson 1978; den Boer 1981; Middleton and Merriam 1981; Merriam 1984; Henderson *et al.* 1985; Wiens 1985; Blondel 1986). In an hierarchical model of populations in a landscape, a set of metapopulations may compose a deme if mating among them is random or a trait

group if mating is random within but not between metapopulations (D.S. Wilson 1980; Rice and Jain 1985; Vrijenhoek 1985; Templeton 1986; Merriam 1987). Considering empirical application of the concepts of a metapopulation and of a deme draws attention to the question of their boundaries. Gene flow across a landscape can establish gene frequency gradients (Roff 1975; Rice and Jain 1985; Vrijenhoek 1985; Gilpin and Soulé 1986; Soulé and Simberloff 1986; Templeton 1986) but sharp boundaries for demes probably are created only by barriers such as large rivers or extensive hostile

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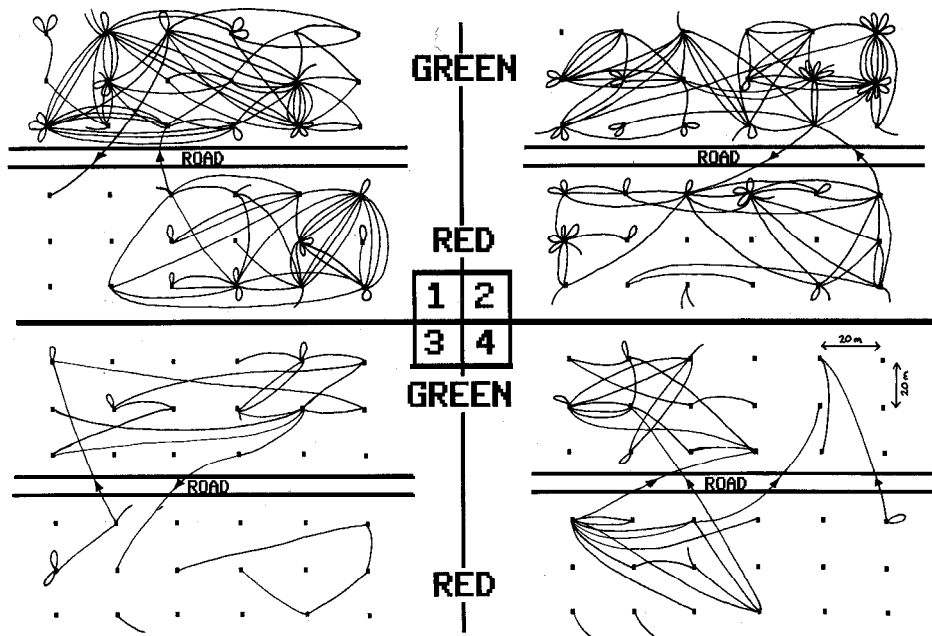


Fig. 1. Movements of white-footed mice within forest bisected by roads and across roads (arrows). (1, 2, 3, 4— study areas).

habitats. For metapopulations there are no data on differences between flow rates of individuals between patches in adjacent metapopulations compared to flow rates between patches within a metapopulation. For both individuals and genes, differences in flow rates are describable in terms of isolation which can be modified by corridors affecting connectivity through isolating habitats (Merriam 1984; Osborne 1984; Fahrig and Merriam 1985; Lefkovich and Fahrig 1985; Szacki 1987; Baudry and Merriam 1988). Operationally these metapopulation boundaries must be functions of isolating features of either the environment or social structures that act as barriers through behavioral mediation.

At the metapopulation level, man-made features such as roads or utility corridors through forests could have barrier effects that could put boundaries on metapopulations. This does not require absolute barriers. The degree and selectivity of the barrier (quantitative and qualitative filters) can determine whether the barrier will be effective only in the short-range and short-term or also in the longer range and longer term.

Barriers have been described by several authors (e.g., Meserve 1971; Giger 1973; Joule and Came-

ron 1974; Oxley *et al.* 1974; Schreiber and Graves 1977, Cole 1978; Kozel and Fleharty 1979; Harris 1980; Wilkins 1982; Kozakiewicz 1983; Mader 1984; Swihart and Slade 1984; Geuse *et al.* 1985; Schoenewald-Cox and Bayles 1986; Buechner 1987; Dickman 1987; Hansson 1987) but the results have not been generalized, due to variation in environments and species studied, and due to the need for a conceptual framework in which to interpret and evaluate the results.

Here we present results from studies of potential metapopulation boundaries at the minimum limit of barrier effect where few studies have been done and we interpret these results in terms of their demographic and genetic effectiveness in metapopulations.

Methods

Two different studies were carried out to assess (1) demographic effect of roads as potential barriers, (2) possibilities of genetic differentiation among patchily distributed subpopulations.

Barrier effects of roads were studied approximately 30 km south of Ottawa (Canada) on four

separate study areas, each 1.44 ha, in a forest fragment and bisected by a narrow, gravel road varying in width from 3.3 m to 6.4 m (Fig. 1). Grassy shoulders 1.7 m and 4.5 m wide bordered the roads in areas 1 and 2 respectively. In areas 3 and 4 there were no shoulders and the tree canopy partly overhanging the roads. The traffic intensity was very low on all four roads – lowest in area 1 (less than 1 vehicle per daylight hour) and slightly higher in areas 2, 3 and 4 (about 2 vehicles per daylight hour).

The forest was mainly deciduous, variable in composition between areas but all suitable habitat for *Peromyscus leucopus*. In area 1 one side was dominated by white cedar (*Thuja occidentalis*) with some eastern hemlock (*Tsuga canadensis*), white spruce (*Picea glauca*) and white birch (*Betula papyrifera*). Quaking aspen (*Populus tremuloides*) and bigtooth aspen (*Populus grandidentata*) dominated on the opposite side of the road. In area 2 both sides of the road were sugar maple (*Acer saccharum*) and beech (*Fagus grandifolia*) with some basswood (*Tilia americana*), white elm (*Ulmus americana*) and white oak (*Quercus alba*). In area 3 one side was young (about 20 years) quaking aspen and white birch, with bigtooth aspen, larch (*Larix laricina*) and some white cedar across the road. Study area 4 had bigtooth aspen, white birch, quaking aspen and sugar maple on one side and sugar maple, beech and eastern hemlock across the road.

Live trapping, colored bait and track registry were used simultaneously on all study areas. Live traps (Sherman) were supplied with terylene bedding and sunflower seeds. Colored bait was margarine and flour mixed with finely shredded colored wool (Holisova 1968a, b). Plastic tubes 30 cm by 4 cm were used to protect the bait against rain, to collect feces and to register tracks. Each study area was designated red on one side of the road and green on the other according to bait color.

Live traps and bait tubes were placed in three lines 120 m long on each side of the road. Each line had six live traps at 20 m intervals with lines 20 m apart, including the pair of lines bordering the roads, and with five bait tubes between the traps along each line.

Studies were carried out from September 17 to

October 22, 1987, Areas 1 and 2 were trapped for three 8-day-periods with 4- and 8-day intervals between them (1440 trap nights, 146 and 167 captures, respectively). In areas 3 and 4 data collection began with the second of these trapping periods (31 and 51 captures, respectively). Feces were collected, tracks identified to confirm feces identity and tubes rebaited every four days during the whole study period. From October 3 (middle of second trapping period) feces were also collected from individuals caught in live traps (if possible). All feces were examined for colored wool fibers under a dissecting microscope.

Live traps were inspected once daily and white-footed mice (*Peromyscus leucopus*) were eartagged with monel fingerling tags and date, location, sex, and mass were recorded at each capture. Males with enlarged testes and females with visible signs of pregnancy or lactation were recorded as sexually active. Three age groups were distinguished by pelage for white-footed mice (Layne 1968). All individuals were released at the point of capture.

During the study 115 white-footed mice were caught 395 times (Fig. 3). From baited tubes, 1526 fecal pellets were collected and 80 fecal pellets were collected from 44 live-trapped individuals.

The genetic study was done south of Ottawa, Canada in deciduous forest fragments in medium intensity farmland growing a mix of hay, pasture, small grains and corn on a plain of moderately heavy soils. These 11 fragments (3 to 25 ha) were selected from a larger sample of fragments chosen specifically to have no fencerow corridors connecting them to other wooded patches. These 11 fragments were also geographically isolated from each other by an average of 5 km and were evenly spread over about 25 x 15 km of farmland with intervening cropland and many roads (2 lane gravel to small provincial highway) as potential barriers. From each forest fragment 10 *P. leucopus* (range 11 to 50%, mode 30% of estimated populations) were live-trapped between 27 June and 2 August 1985. For each mouse a blunted syringe was used to inject a few drops of distilled water into the mouth and then extract a saliva sample. Samples were stored on ice in the field and at -20°C in the laboratory and were processed according to Aquadro and

Table 1. Distances (m) moved between traps by white-footed mice. G, R = green, red sides of road. 36 day Max, 24 day Max, 1 day Max = maximum distances moved when measured over 36-, 24- and 1-day-periods.

Study area	1		2		3		4	
	G	R	G	R	G	R	G	R
No. captures	88		83		33		49	
Mean	34.7	36.2	30.7	35.3	42.1	33.6	38.0	45.7
36 day Max	72.1	80.0	107.7	80.0				
24 day Max					102.0	63.3	63.3	89.4
1 day Max	72.1	80.0	60.0	56.6	82.5	63.3	63.3	89.4

Patton (1980). Electrophoresis was done in vertical gel cells using single layer 6% acrylamide gels in a continuous glycine-sodium glycinate buffer at pH 8.3. After incubation with an agar overlay and staining by potassium iodide, the electromorphs were visible, and separation was clear and consistent.

Results

Movements of tagged white-footed mice among traps were frequent within all study areas separated by the roads (Fig. 1). Individuals commonly moved distances which would have been sufficient to cross the roads (Table 1). There was no relationship evident between width of road or traffic volume and numbers of mice crossing. Maximum sampling time (36 d for areas 1 and 2, 24 d for areas 3 and 4) produced longer maximum movement distances in only three cases compared to maximum distances revealed after only one day (Table 1).

Movements across the roads were very infrequent (Table 2) although the frequency and extent of movements between traps in the forest on either side of the road (Fig. 1) would predict a much higher number of crossings. Only the barrier effects of the road on the behavior of the animals distinguishes the movement between the two trap lines adjacent to the road from the very frequent movements between other lines or pairs of traps (Fig. 1). During the whole study only nine from among 115 marked individuals of white-footed mice (7.9%), were shown to have crossed the roads (one twice) (Table 2, Fig. 1).

Considering each study area separately, percentages of tagged white-footed mice crossing the road were lower in areas 1 and 2 (5.4% and 1.9% respectively) while they were distinctly higher in areas 3 and 4 (25% and 22.5% respectively). No relationships were evident between numbers of mice crossing the road and population numbers (as indicated by numbers of mice captured).

Percentages of feces containing the bait from the opposite side of the road were also very low: in study areas 1 and 2 about 1% and in study areas 3 and 4 about 5% (Fig. 2).

Male and female white-footed mice crossed the roads but males predominated and all males in this group were sexually inactive adults (seasonal norm) (Table 2). From among three females crossing the roads two were lactating and one was just entering the subadult class, the only non-adult crossing the road (Table 2). This individual was trapped several times after crossing the road and apparently established its new home range on the other side. Trap mortality was higher for mice crossing roads (5 of 9 = 55%) than for captures not associated with crossings (17 of 106 = 16%). In area 4, all four mice died in traps after crossing the road although they had survived one to six previous captures (Table 2). This mortality reduced potential return crossings but is uninterpretable due to numbers and lack of further data.

Compared to characteristics of all others (Fig. 3, Table 2), white-footed mice crossing the roads were different in sex ratio (2.0 vs 1.2), age structure (mostly adults, only one juvenile) and reproductive condition (lack of adult non-reproducing females).

Table 2. Characteristics of *Peromyscus leucopus* crossing the road.

Study area	Sex	Sexual activity	Age group	Movements from to	Mean body weight (g)	Number of captures	Comments
1	F	lactating	ad	red to green	21.5	2	
1	M	(-)	ad	green to red	22.3	2	
2	M	(-)	ad	red to green to red	15.0	4	
3	F	lactating	ad	green to red	17.0	3	died in trap
3	F	(-)	juv	red to green	12.0	5	
4	M	(-)	ad	red to green	18.7	5	died in trap
4	M	(-)	ad	green to red	15.4	7	died in trap
4	M	(-)	ad	green to red	19.0	2	died in trap
4	M	(-)	ad	green to red	17.0	4	died in trap

(-) sexually inactive, (+) sexually active.

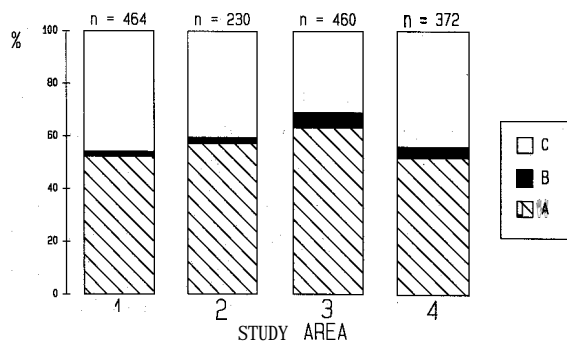


Fig. 2. Occurrence of colored bait in feces from each study area. 1, 2, 3, 4 = number of study area, n = numbers of fecal pellets examined. A = color from side of road where collected, B = color from opposite side of road, C = no color.

Mean body weight of individuals crossing the roads (18.2 g for adults) as well as mean number of captures per individual (3.8) were similar to those found for all others (Table 2).

The genetic study used three electrophoretic variants of salivary amylases designated as fast, medium and slow (Evans *et al.* 1977; Aquadro and Patton 1980). These mice were predominantly homozygous for the medium variant and showed relatively low variation in allele frequencies (Table 3). The fixation index (F_{st} of Wright 1978; Rockwell and Barrowclough 1987) was calculated to be 0.0552 ($F_{IS} = .0880$, $F_{IT} = -.0280$). This value is not significant ($\chi^2 = 2N(F_{st}) = 15.79$) and indicates very little genetic differentiation, assuming that these patch populations have a demic structure in the sense of Wright (1931). The mean of Nei's

genetic identity, I , a measure of genetic similarity among the populations, was 0.9764 for the 11 forest fragments which gives an index of genetic distance $D = 0.0239$ (Fristrom and Spieth 1980). These results are not independent but for salivary amylases all do indicate a lack of genetic isolation among the 11 forest fragments. Ongoing studies of mitochondrial DNA (Tsuchiya and Merriam) will assess the generality of these results.

Discussion

The effect of these roads as selective filters is not statistically demonstrable because the largest expected frequencies for age:sex combinations crossing the roads are small. However Fig. 3 and Table 2 make clear that if there was any filtering, it was preventing crossing by the 36% of trapped animals that were subadults and juveniles and probably was most effective against subadults which were 22% of the trapped sample but were unrepresented in the sample crossing roads. In terms of repopulating local extinctions, pregnant females could be the most valuable colonists. Crossings by lactating females, the lack of subadults and juveniles, and the normal body weights of mice that crossed, are not the characteristics of dispersers predicted by the literature (Healey 1966; Fairbairn 1976, 1978a, 1978b, Hansen and Batzli 1978).

These narrow unpaved country roads did have a quantitative barrier effect. Many fewer mice

Table 3. Salivary amylase electromorph frequencies in *Peromyscus leucopus* from 11 eastern Ontario forest fragments isolated from other forest fragments by low connectivity of landscape pattern.

Forest Fragment	Amylase electromorphs*						Allele frequency		
	ff	fm	fs	mm	ms	ss	f	m	s
1	0	4	0	10	1	1	0.13	0.78	0.09
2	1	4	0	5	0	0	0.30	0.70	0.00
3	0	4	0	9	1	0	0.14	0.82	0.04
4	0	5	0	11	5	0	0.12	0.76	0.12
5	0	1	0	6	0	0	0.07	0.93	0.00
6	0	3	0	4	0	0	0.21	0.79	0.00
7	1	1	0	13	0	0	0.10	0.90	0.00
8	0	7	0	10	0	0	0.21	0.79	0.00
9	1	5	0	6	1	1	0.25	0.64	0.11
10	0	2	0	10	0	0	0.08	0.92	0.00
11	0	7	0	3	0	0	0.35	0.65	0.00

* Designated as fast (ff), medium (mm), slow (ss) and heterozygous combinations.

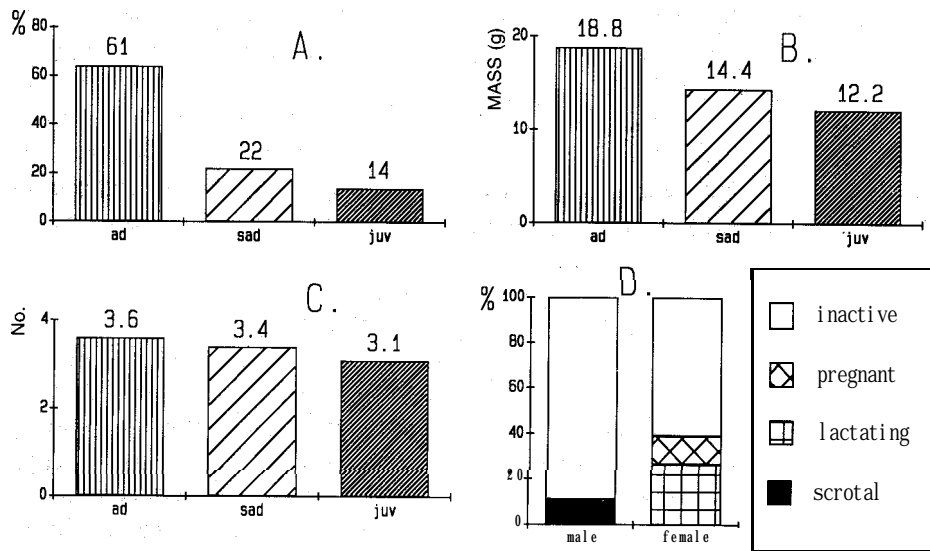


Fig. 3. Some characteristics of white-footed mice tagged in all study plots (see Table 2 for sex ratios): (a) age structure (ad-adult, sad-subadult, juv-juvenile), (b) mean body weight, (c) mean number of captures per individual, (d) reproductive condition.

crossed the roads than moved an equal distance in the forest alongside the road (Fig. 1, Table 2). These roads, unlike Mader's (1984) small forest road, were not absolute barriers but were effective inhibitors of movements as was the dirt track studied by Swihart and Slade (1984). Oxley *et al.* (1974) studied two-lane gravel roads which were 11.0 and 14.6 m wide and more heavily travelled (5/h) than roads studied here. They found no crossings by any of eight mice at one road and seven

crossings from among 26 mice marked at the other. There was no clear relationship between barrier effect and road width or traffic volume in our study and there is no apparent distinction between the roads we have studied and the two gravel roads studied by Oxley *et al.* (1974). Swihart and Slade (1984) found no change in inhibitory effect when a dirt track was widened to 3.6 M and graveled. It is possible, but not certain, that the frequency of crossings by *P. leucopus* differed significantly for

the next three larger, paved roads studied by Oxley *et al.* (12 m, 12 vehicles/h; 27 m, 26/h and 31 m, 200/h).

Bakowski and Kozakiewicz (1988) have found that a 5 m wide road through forest in northern Poland acts as a quantitative barrier but not a qualitative filter for age, sex or condition of bank voles (*Clethrionomys glareolus*). Movements of voles across the road were very infrequent but almost all individuals translocated across the road, returned to their original side. For yellow-necked mice (*Apodemus flavicollis*), the same road acted neither as a barrier nor as a filter.

The important point is that we have no way of judging the importance of any particular difference or frequency of crossings except by reference to some process question at particular scales of space and time. The questions could be about home range behavior of individual mice, on a daily or weekly basis or about demography of metapopulations over a generation length, or about changes in gene frequency over several generations. Selecting one of these foci permits some judgment about importance of barrier effects and such barrier effects are critical parameters of conceptual models at each of these hierarchical levels. For example, there were demonstrable barrier effects for the four small roads we studied and for the two gravel roads and the three smallest paved roads studied by Oxley *et al.* (1974); individual home range behavior could be affected in all cases. The same was true for *Clethrionomys* studied by Bakowski and Kozakiewicz (1988) but no effect was shown for *Apodemus flavicollis*. At the demographic level, all these roads were not effective barriers for stopping recolonization of empty habitat caused by a local extinction on the other side of the road; they could not form a metapopulation boundary. Given that judgment it also is clear that they were not effective barriers to gene flow and therefore could not constitute a demic boundary unless changes in population along the barrier changed so that the barrier effect was modified. Hence the two superhighways studied by Oxley *et al.* (1974) might act as metapopulation boundaries (no crossings by *P. leucopus*) but could not be judged to be effective demic boundaries because they were studied for only a fraction of a 4.5

month period and gene frequency changes could be controlled by gene flow too low to be detected by this sampling. Mader's (1984) study of a 4.5 m paved road and a 3 m paved forest road found that *Apodemus flavicollis* crossed both roads frequently enough potentially to repopulate a local extinction (although half the individuals crossing had been translocated across road C). For a 6 m, paved, two-lane road with 250 vehicles/h, Mader (1984) found no crossings by small mammals. This degree of barrier effect could well prevent repopulation of a local extinction or bound a metapopulation and possibly, but by no means certainly, also reduce gene flow sufficiently to bound a deme.

Data from our study of salivary amylases show that results applicable at the level of patch and metapopulation demography are not necessarily applicable at the level of the genetic deme or trait group. The 11 forest fragments we studied were part of a sample of 22 wooded patches chosen to be as isolated as possible from other patches. Over a two-year-period winter mortality caused local extinctions in spring in 2% to 10% of the populations in these patches (Merriam and Wegner SCOPE Ecotones Conf., Paris, Dec. 1988). Based on these local extinction rates and on the low connectedness of the patches by fencerows, this sample was considered to be biased toward being demographically isolated patches. The scattered distribution of these patches in about 375 km² of farmland mosaic with both natural and man-made barriers elevated the potential isolation to the regional scale. But the salivary amylase data indicate that the 11 patch populations studied genetically could be a single interbreeding genetic population (Table 3). Although the clustering algorithm in the BIOSYS program shows some genetic substructuring in the 11 populations (J.M. Novak, pers. comm.), those clusters are almost totally out of register and make no sense in terms of the geographic clustering of the patches. Apparently, demographic and genetic structuring in this hierarchy must be treated separately until more is known.

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