Population subdivision of house mice (*Mus musculus*) in an agrarian landscape: consequences for control

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Abstract: In Argentinean agroecosystems, house mice (*Mus musculus* L., 1758) show a discontinuous distribution, with high abundances in farms but scarce abundance in crop fields. In our study area, the abundance of *M. musculus* could be affected by their movements among farms. We hypothesize that (1) *M. musculus* do not move among farms versus (2) *M. musculus* do move among farms. Furthermore, based on our second hypothesis, *M. musculus* move actively (hypothesis 2.1) or passively by human transport (hypothesis 2.2). Based on hypothesis 1, we predict that genetic subdivision will exist among farms and that genetic divergence will be independent of geographic distance. Based on hypothesis 2.1, genetic differentiation will be correlated with geographic distance. Based on hypothesis 2.2, genetic subdivision will be absent, or genetic differentiation will be related to human movements. We examined genetic variation among farms (n = 15) using ~~six~~ microsatellite loci and tracked the movements of 36 individuals from five farms with fluorescent powders. Populations of *M. musculus* showed genetic differentiation at both farm and shed scales. Genetic and geographic distances were significantly correlated. There was no evidence of passive movements of *M. musculus*. The movements of 36 *M. musculus* within farms, tracked with fluorescent powder, were short. According to these results, hypothesis 2.1 is favoured.

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range of habitats, including commensal, rural, and sylvan environments, whereas in other places *M. musculus* exists essentially as a number of relatively isolated populations, especially near human habitation (Pocock et al. 2005). The range of habitats used depends on the spatial structure of the physical and biotic characteristics of the environment, such as the availability of resources, and the presence of predators and competitors. *Mus musculus* competes poorly with other rodents in outdoor situations, and when there is an established community of sylvan rodents, *M. musculus* is restricted to commensal habitats. However, when other rodent species are scarce and climatic conditions are favourable, *M. musculus* can become a rural pest (Jacob et al. 2003; Brown 2005; Busch et al. 2005).

Human activities frequently create a patchy distribution of favourable habitats that may be exploited by a metapopulation of *M. musculus* (Smith 1994). Depending on the environmental context and the spatial heterogeneity, the persistence of populations of *M. musculus* is mainly determined by local factors of the favourable patches, or may be promoted by migration among patches through an environment where resources may be limited (Smith 1994) or where *M. musculus* competes with the other small-mammal species (Pocock et al. 2004).

Agrarian ecosystems in the pampean region of Argentina are spatially heterogeneous, with a matrix of crop fields and pastures surrounded by weedy margins along roads, as well as small patches of woodlots and riparian habitats (Busch and Kravetz 1992; Bonaventura and Cagnoni 1995). Poultry activity has increased in the last 30 years, with poultry farms generally isolated and surrounded by crop fields. In this system, *M. musculus* is present essentially as a number of relatively isolated populations on farms, as *M. musculus* is scarce in crop fields and other habitats, where *M. musculus* competes with native rodents (Busch et al. 2005).

In farms, *M. musculus* is considered a pest because it can achieve high abundance and causes losses in chicken feed, damage to buildings, and may carry diseases to both humans and domestic animals (Acha and Szyfres 1992). Farm owners control the abundance of *M. musculus* mainly by maintaining hygiene and sanitary conditions and also by chemical control with rodenticides; however, in spite of these measures, *M. musculus* is present in almost all farms in the area (León et al. 2007).

Rodent control on each farm is performed independently and at different times; consequently, treated farms may be recolonized from nontreated ones. The probability of recolonization may depend on the range of movements of *M. musculus*. If *M. musculus* is able to move freely across rural habitats, farm populations should be widely connected and show common dynamics. However, if movements are restricted, different farms should host subpopulations of a metapopulation (Hanski and Gilpin 1997; Ritche 1997). A third alternative is that farm populations are completely isolated, with no interchange of individuals between them. In each case, the implementation of control measures should involve different spatial scales. In the first two cases, the unit of control should be larger than one farm (Abdelkrim et al. 2005), whereas in the third case, the control of individual farms should be enough to achieve success (Robertson and Gemmel 2004; Abdelkrim et al. 2005). The definition of the control unit may also change if rodents move by themselves or if they are carried by humans, because recolonization would be associated with human movements.

Connectivity between different portions of a population distributed in a spatially heterogeneous environment may be assessed either by direct estimation of movements and (or) by indirect methods. Molecular genetics has provided a valuable means of identifying units of conservation, management, and evolutionary significance (Moritz et al. 1996).

The degree of genetic structure within a population is indicative of connectivity. Negligible genetic differentiation between spatially isolated populations is indicative of significant gene flow, whereas significant differentiation between adjacent populations indicates limited dispersal (Robertson and Gemmel 2004). However, dispersal rates depend on the distance between subpopulations, and if *M. musculus* move by themselves, there will be a correlation between genetic divergence and geographic distance (Wright 1943; Ryan et al. 1993). Variation in microsatellites has proven useful to assess genetic differentiation at small geographic scales (Shaw et al. 1999), because their high rates of mutation (and therefore polymorphism) enhances the power for testing population differentiation (Rousset and Raymond 1995).

Molecular markers provide an indirect measure of movements because genetic subdivision depends not only on movements but also on successful reproduction of immigrants, which is frequently limited in territorial species such as *M. musculus* (Dallas et al. 1995). More direct estimations of movements are based on the tracking of marked individuals, such as capture–mark–recapture methods, radio-tracking (Cochran and Lord 1963; Slade and Russell 1998), and the technique of marking with fluorescent powders (Lemen and Freeman 1985). The first method relies on high recapture rates (Hayne 1949), which makes the method difficult to apply to *M. musculus* (Drickamer et al. 1999; Aplin and Singleton 2003), and radio-tracking is expensive, whereas the technique of using fluorescent powders is more economical and has been used successfully to estimate the range of movements of small rodents in different environments (Jike et al. 1988; Nicolas and Colyn 2007). For example, Mikesic and Drickamer (1992) obtained similar estimates of home ranges of adult *M. musculus* using powder and radio-tracking techniques.

Results from both direct and indirect methods suggest that the range of movements of *M. musculus* is highly variable depending on environmental conditions and on individual characteristics. Whereas in some cases this species has shown limited genetic flow among demes (Anderson 1964, 1970; Reimer and Petras 1967; Singleton and Hay 1983; Berry 1986; Ryan et al. 1993; Dallas et al. 1995) and a small range of movements in commensal habitats (Selander 1970; Pocock et al. 2005), other studies have suggested that *M. musculus* may travel large distances (Berry and Jakobson 1974; Myers 1974).

Because range of movements of *M. musculus* may determine the scale of the appropriate measures of control, and no information exists regarding the movements and genetic structure of its populations in our study area, we assess the following hypotheses: (1) *M. musculus* do not move among different farms versus (2) *M. musculus* do move among farms. Based on hypothesis 2, *M. musculus* move either ac-

tively (hypothesis 2.1) or passively by human transport (hypothesis 2.2). Therefore, based on hypothesis 1, we predict that genetic subdivision will exist among farms and that genetic divergence will be independent of the geographic distance. Based on hypothesis 2.1, genetic subdivision will exist among farms and that genetic differentiation will be correlated with geographic distance. Based on hypothesis 2.2, genetic subdivision will be absent, or genetic differentiation will be related to the characteristics of human movements among farms. Thus, at what scale (i.e., individual farm or larger spatial scale) should populations of *M. musculus* be controlled in poultry farms?

Materials and methods

Study area

Fieldwork was conducted in 18 poultry farms located in Exaltación de la Cruz, Buenos Aires Province, Argentina (34°18′S, 59°14′E). Distances between farms were between 200 m and 15 km (Fig. 1). The study area is located in the undulated subregion of the pampean region, and is characterized by a temperate climate with a mean annual temperature of 16 °C and a mean annual precipitation of 1000 mm.

The original grasslands that covered the area were replaced by crop fields and pastures, as well as trees. Presently there are few remaining native-plant communities along crop-field edges, river embankments, and railway terraces. Main crops are soybean, maize, and wheat; other human activities in the area include cattle, horse, and pig breeding, and in the last 30 years, poultry breeding (Miño et al. 2007).

Poultry farms

Poultry farms are placed on lots of 1–4 ha and have a variable number of breeding sheds (3–10, mostly 3). Sheds are rectangular, about 100 m × 10 m, and are separated by unpaved roads and areas covered by vegetation. Within farms, other buildings such as the farmhouse and sheds for materials or food stores provide alternative sources of refuge and food for rodents. Farms are surrounded by wire fences, along which a weed community is frequently observed. In most cases, farms are surrounded by crops or livestock fields. Native rodents are commonly found both along weedy fences and in the surrounding fields. In our study area, farms work with about four different companies that provide the chickens and chicken feed, and these companies are responsible for the commercialisation of poultry industry.

Rodent community

Five sigmodontine species are found in the study area: Azara's grass mouse (*Akodon azarae* (J. Fischer, 1829)), small vesper mouse (*Calomys laucha* (G. Fischer, 1814)), drylands vesper mouse (*Calomys musculinus* (Thomas, 1913)), yellow pygmy rice rat (*Oligoryzomys flavescens* (Waterhouse, 1837)), and red hocicudo (*Oxymycterus rufus* (J. Fischer, 1814)). One caviomorph (*Cavia aperea* Erxleben, 1777) and three murine species (*M. musculus*, Norway rat (*Rattus norvegicus* (Berkenhout, 1769)), and black rat (*Rattus rattus* (L., 1758))) are also found in the study area. *Calomys laucha* is numerically dominant in crop fields, whereas *A. azarae*, *O. flavescens*, *O. rufus*, *C. aperea*, and *C. musculinus* are more abundant in field edges and in less disturbed areas (Mills et al. 1991; Busch and Kravetz 1992; Bilenca et al. 1995). Commensal species such as *M. musculus* and *Rattus* spp. are dominant in peridomestic habitats and in poultry farms, but are rare in crop fields and sylvan habitats (Kravetz et al. 1987; Miño et al. 2001). On farms, *M. musculus* and *Rattus* spp. are mainly present around poultry sheds, whereas sylvan species are mostly present in the weedy edges that limit the farms (Miño et al. 2007).

Genetic studies

We used the genetic subdivisions of the populations of poultry farms as an indirect method of estimating movements. This method summarizes events that have occurred over many generations and covers a temporal and spatial scale that is difficult to achieve by recapture methods, especially in the case of *M. musculus*, which has low recapture rates. Also, it was difficult to conduct more long-term recapture samplings for this study because farmers did not want animals released onto their farms after capture.

Sherman traps were placed around every shed in each of 15 poultry farms (1, 2, 3, 5, 8, 21, 22, 24, 25, 27, 28, 29, 30, 31, and 32; Fig. 1) between December 2004 and May 2005 to capture rodents for tissue samples. From each individual *M. musculus* captured, we took about 1 cm of the tip of the tail that was preserved in 90% alcohol for later analysis in the laboratory. We obtained between 7 and 11 samples per farm (Table 1).

We used the microsatellites *D1mit122*, ~~*D2mit511*~~, *D3mit312*, *D4mit185*, *D5mit16*, and *Mmu-2* as molecular markers. They were taken from the database of the Whitehead Institute for Biomedical Research (http://www.genome.wi.mit.edu; accessed ~~DAY MONTH YEAR).~~ These loci were selected based on the reported levels of polymorphism; only one locus per chromosome pair was screened.

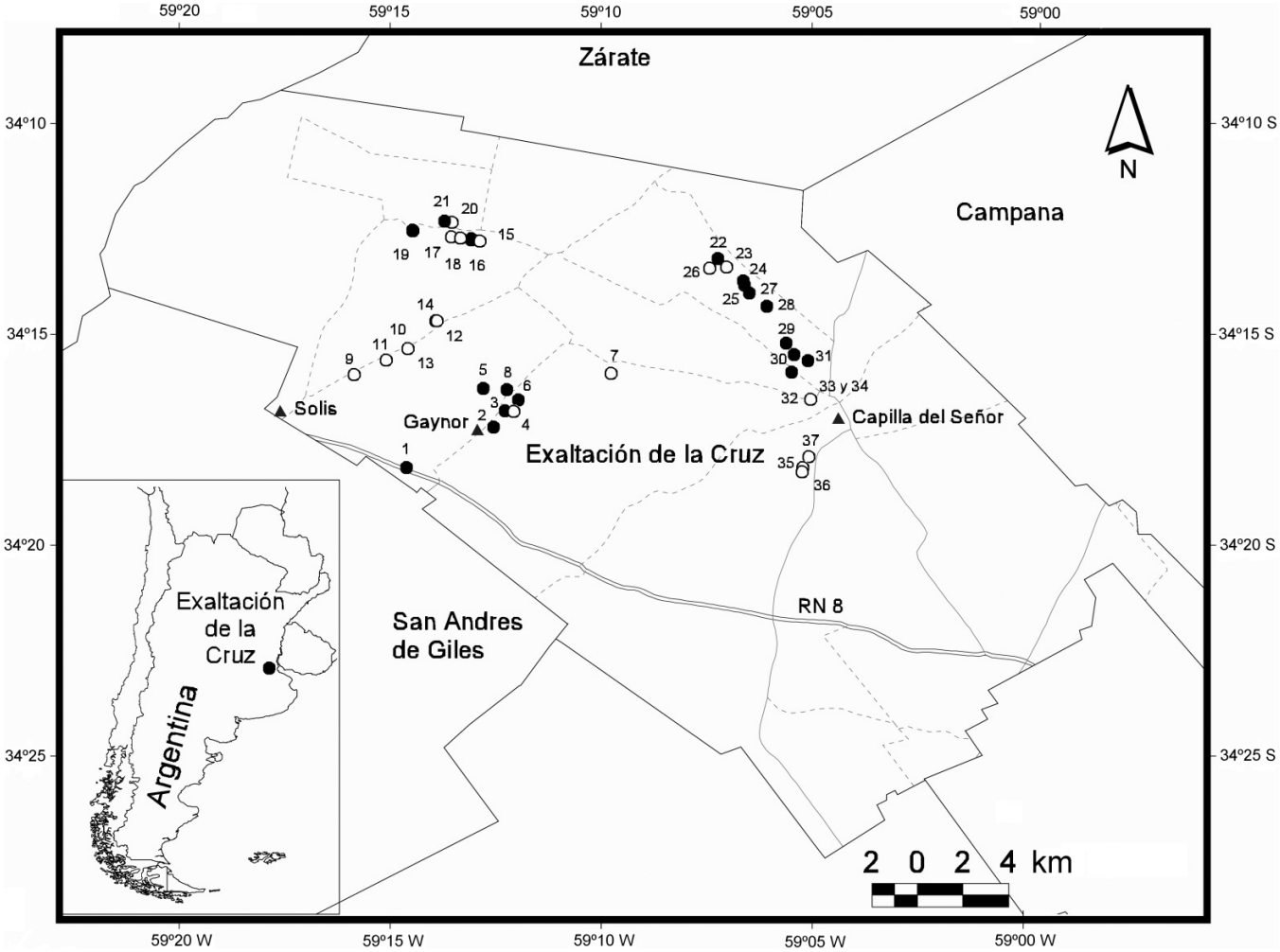
DNA extraction was performed by the method described in Levitan and Grosberg (1993). Amplification of nuclear microsatellite loci was achieved by polymerase chain reaction (PCR). Following amplification, PCR products were resolved by electrophoresis on 8% native polyacrylamide gels together with a 10-base-pair molecular marker, stained with SYBR green (QIAGEN Inc., Mississauga, Ontario, Canada), and photographed.

Allele frequencies were calculated with FSTAT version 2.9.3.2 (Goudet 2002), which was also used to estimate the mean number of alleles per locus and allele richness. Allele richness estimates the number of alleles independently of the sample size. Mean number of expected (mean H_e) and observed (mean H_o) heterozygosities for each farm were calculated with TFPGA version 1.3 (Miller 2000).

Differences between mean H_e and mean H_o were assessed with a test of scores using the U statistic (Rousset and Raymond 1995). The alternative hypotheses of excess or deficiency in heterozygotes were analysed with GENEPOP version 1.2 (Rousset and Raymond 1995).

Wright's F statistics (Wright 1965, 1978) were estimated according to Weir and Cockerham (1984), where θ is an estimator of F_{ST}, f estimates F_{IS}, and F estimates F_{IT}. For these calculations, we used FSTAT version 2.9.3.2 (Goudet

Fig. 1. Location of poultry farms (● and ○) in the study area. Solid circles indicate farms where house mice (*Mus musculus*) were captured.



2002). F_{ST} is a measure of population subdivision at the farm level, whereas F_{IT} estimates the deficiency or excess of heterozygotes in the whole population, and F_{IS} is the degree of inbreeding within subpopulations. Each parameter was estimated for each locus considered and then averaged through all loci.

Population subdivision among sheds within each farm was assessed in eight farms. We used the farms with more than five samples (individuals) per shed (farms 1, 2, 5, 21, 25, 27, 29, and 30; Fig. 1). We estimated F_{ST} using TFPGA version 1.3 (Miller 2000).

Correlations between matrices of the two types of pairwise distances among farms (matrix of F_{ST} and matrix of geographic distance) were analysed using the Mantel test in TFPGA (Miller 2000).

We compared the values of F_{ST} between pairs of farms that work with the same company and pairs of farms that work with different companies with the Mann–Whitney *U* test (STATISTICA version 7.0; StatSoft, Inc., Tulsa, Oklahoma, USA). This analysis was performed for all farms for which we knew the company that provided the chickens (farms 1, 2, 3, 5, 7, 9, 10, 11, 12, 14; Fig. 1).

Direct study of movements

To directly estimate movements within farms, we tracked rodents marked with fluorescent powders (Lemen and Freeman 1985). We used this technique because of limitations imposed by farmers in using other mark–recapture methods. Also, a previous work conducted in farms of the study area with mark–recapture and radio-tracking methods (D.M. Valenzuela, unpublished data) showed low recapture rates of *M. musculus*.

Rodents were captured in five poultry farms (farms 2, 5, 7, 16, and 19; Fig. 1) using Sherman traps placed along the walls of the breeding sheds. Samplings were conducted seasonally between May 2007 and February 2008.

After capture, rodents were placed in a nylon bag containing a small quantity of fluorescent powder (Radiant color, Richmond, California, USA) of different colour for each individual. For each animal, we recorded the date and site of capture, the sex, corporal and tail lengths, body mass, and reproductive status. *Mus musculus* of each sex were classified into three age classes according to body mass: juvenile females (≤10.5 g), juvenile males (≤11 g), subadult females (≥11 and ≤ 15.5 g), subadult males (≥11.5 and ≤ 16.5 g), adult females (≥16 g), and adult males (≥17 g) (Drickamer

Table 1. Allele frequencies, ~~mean number of~~ expected ~~heterozygotes~~ (mean H_e), ~~mean number of~~ observed ~~heterozygotes~~ (mean H_o), mean number of alleles per locus, and allele richness for each poultry farm.

	Farm ID. and sample size of *M. musculus*														
Allele	1 (12)	2 (14)	3 (7)	5 (13)	8 (10)	21 (11)	22 (10)	24 (8)	25 (15)	27 (6)	28 (16)	29 (16)	30 (10)	31 (11)	32 (6)
D1mit122															
1	—	—	—	—	—	—	—	0.07	—	—	—	—	0.10	—	—
2	0.08	0.03	—	0.19	0.16	0.36	0.40	0.14	0.43	0.08	0.20	0.56	0.40	0.50	0.25
3	0.08	0.21	0.07	0.35	0.28	—	0.30	0.29	0.30	0.25	0.50	0.10	0.20	0.35	0.50
4	0.27	0.25	0.36	0.39	0.17	0.09	0.10	0.29	0.20	0.17	0.07	0.07	0.10	0.05	0.08
5	0.35	0.43	0.57	0.08	0.28	0.55	0.20	0.21	0.07	0.50	0.23	0.27	0.20	0.10	0.17
6	0.19	—	—	—	—	—	—	—	—	—	—	—	—	—	—
7	0.03	0.04	—	—	—	—	—	—	—	—	—	—	—	—	—
8	—	0.04	—	—	0.11	—	—	—	—	—	—	—	—	—	—
D4mit185															
1	—	0.03	0.07	0.04	0.06	—	0.45	0.07	0.19	0.10	0.03	0.28	0.05	0.22	—
2	0.46	0.90	0.93	0.40	0.50	0.27	0.15	0.07	0.04	—	0.30	0.16	0.10	—	0.17
3	0.23	0.07	—	0.36	0.31	0.18	0.05	0.21	0.22	0.90	0.23	0.03	0.50	0.17	0.33
4	—	—	—	0.10	0.13	0.23	0.05	0.43	0.35	—	0.27	0.34	0.10	0.39	0.42
5	0.31	—	—	0.10		0.32	0.30	0.21	0.19	—	0.17	0.19	0.25	0.22	0.08
D3mit312															
1	0.04	0.03	—	—	—	—	—	—	—	—	—	—	—	—	—
2	0.23	0.63	0.65	0.08	0.10	0.82	0.45	0.43	0.50	0.70	0.50	0.46	—	0.55	0.50
3	0.46	0.17	0.14	0.50	0.30	0.18	0.25	0.21	0.32	0.10	0.25	0.15	0.25	0.15	0.42
4	0.27	0.17	0.21	0.38	0.60	—	0.30	0.36	0.18	0.20	0.25	0.39	0.75	0.30	0.08
D5mit16															
1	—	—	—	—	—	—	—	—	—	0.08	0.03	0.09	0.35	0.30	0.25
2	0.71	0.68	0.93	0.88	0.75	0.64	0.75	0.28	0.23	0.17	0.53	0.34	0.15	0.30	0.25
3	0.29	0.14	—	0.12	0.20	0.27	0.10	0.36	0.53	0.50	0.16	0.50	0.40	0.35	0.50
4	—	0.18	0.07	—	0.05	0.09	0.15	0.36	0.23	0.25	0.22	0.06	0.10	0.05	—
Mmu-2															
1	—	0.11	—	—	—	—	—	—	—	—	—	—	—	—	—
2	0.09	—	—	0.12	0.25	—	0.20	—	0.33	0.08	0.09	0.04	0.10	—	—
3	0.09	0.11	—	0.25	0.55	0.09	0.40	0.71	0.22	0.25	0.27	0.35	0.05	0.11	0.25
4	0.23	0.61	0.21	0.50	0.15	0.32	0.25	0.07	0.28	0.50	0.36	0.53	0.40	0.28	0.17
5	0.59	0.17	0.71	0.12	0.05	0.32	0.05	0.21	0.11	0.08	0.04	0.08	0.40	0.61	0.50
6	—	—	0.07	—	—	0.27	0.10	—	0.05	0.08	0.14	—	0.05	—	0.08
7	—	—	—	—	—	—	—	—	—	—	0.09	—	—	—	—
Mean H_e	0.64	0.52	0.38	0.59	0.63	0.59	0.69	0.64	0.70	0.57	0.70	0.65	0.66	0.66	0.69
Mean H_o	0.60	0.39	0.37	0.56	0.49	0.60	0.60	0.64	0.68	0.52	0.68	0.62	0.56	0.54	0.62
Mean no. of alleles	3.8	4	2.6	3.6	3.8	3.2	4	3.8	4	3.6	4.4	4	4.2	3.6	3.6
Allele richness	3.2	3.1	2.4	3.1	3.4	3	3.6	3.5	3.6	3.4	3.7	3.3	3.6	3.3	3.5

et al. 1999). Animals were then released at the site of capture, and the coloured track was recorded after two nights using UV lights. We registered the length and location of the displacements.

We compared the length of movements by sex and age class (between subadults and adults, because of the low number of juveniles captured) using a two-factor ANOVA (STATISTICA version 7.0).

Results

Genetic studies

We found a total of 28 alleles for the five microsatellite loci (Table 1) analysed in 168 *M. musculus* from 15 poultry farms. The frequencies of each allele per loci are shown in Table 1.

For all farms the mean H_e varied between 0.38 and 0.70, whereas the mean H_o varied between 0.37 and 0.68 (Table 1). Farm 3 showed the fewest number of heterozygotes. The mean number of alleles per locus ranged from 2.6 and 4.4; the allele richness varied between 2.4 and 3.7 (Table 1). In terms of the mean number of alleles per locus and allele richness, farm 3 was the least variable.

The studied loci were highly polymorphic. The H_e per locus varied between 0.55 and 0.71, with a mean of 0.63, whereas the H_o per locus varied between 0.49 and 0.64,

with a mean of 0.56. The number of alleles per locus ranged between 4 and 8 (Table 2).

The allele frequencies of *D3mit132*, *D1mit122*, and *Mmu2* were significantly different from the expected frequencies according to a Hardy–Weinberg distribution ($p < 0.05$). These departures were mainly due to results from farm 29 in *D1mit122* and farms 2 and 8 in *Mmu2*, whereas farm 30 showed deviations from Hardy–Weinberg in *D3mit132*, *D1mit122*, and *Mmu2*. In all cases, departures from Hardy–Weinberg were caused by a deficiency in heterozygotes, as shown by the positive and significant values of the f parameter for the three loci (Table 2).

According to the value of θ for each loci and for the global analysis, there was a genetic subdivision in the population of *M. musculus* among poultry farms ($\theta = 0.124$, $p < 0.01$; Table 2). However, the parameter f, which estimates the F_{IS} index, was significant in 3 of 5 loci and for the global analysis, indicating the absence of random breeding ($f = 0.104$, $p = 0.01$; Table 2). The total population showed a deficit in heterozygotes with respect to Hardy–Weinberg equilibrium ($F = 0.216$, $p = 0.01$; Table 2).

There was a significant and positive correlation between genetic differentiation and geographic distance (Mantel test, $r = 0.806$, $p = 0.01$; Fig. 2), suggesting that most gene flow occurs among nearby populations.

There was no significant difference in the values of F_{ST} between the group of pairs of farms that work with the same company and the pairs of farms that work with different companies (farms that share a company: median = 0.20; farms that do not share a company: median = 0.15; Mann–Whitney U test, $U_{[33,12]} = 309.57$, $p = 0.39$), suggesting that genetic differences among farms are not due to human transport of chickens or ~~of~~ their food.

According to the value of θ for the global analysis, there was a significant genetic subdivision in the population of *M. musculus* at the shed level ($\theta = 0.14$, $p < 0.01$), suggesting that effective dispersal within farms is also limited.

Direct study of movements

We recorded the movements of 36 individual *M. musculus*. In all cases the tracks were observed along the wall of the sheds near the floor, or in the wire cloth that continues the wall up to the ceiling, or in the canvas that covers the wall. Movements were linear, parallel to the shed walls, and at a short distance from them. We did not record tracks towards other sheds or to the perimeter of the farm. Nine of 36 tracks followed ended in burrows, placed underground near the shed walls. Some tracks disappeared into the shed and then reappeared at a short distance outside. On a few occasions, we recorded tracks along the interior wall of the shed, but we only had access to the interior when the chickens were absent.

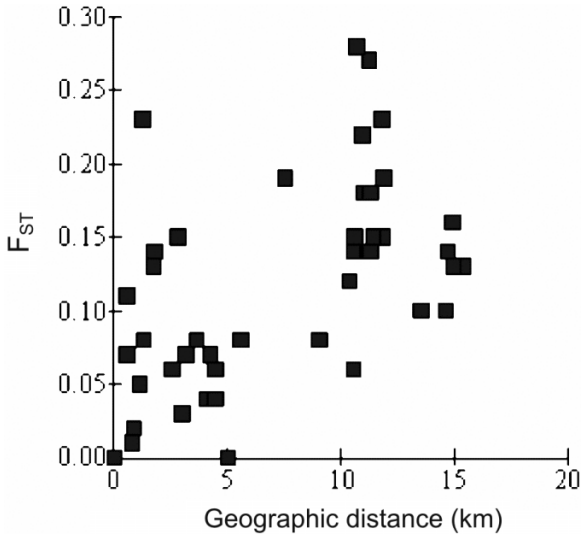
The range of movements recorded was between 1.55 and 58 m, with a mean of 11.7 m (~~SD~~ = 9.31) for males and 12.34 m (~~SD~~ = 13.46) for females. There were no significant differences based on sex or age in the range of movements (sex: $F_{[1,29]} = 0.014$, $p = 0.9$; age class: $F_{[1,29]} = 0.017$, $p = 0.89$; sex × age class interaction: $F_{[1,29]} = 0.18$, $p = 0.74$).

Table 2. Estimates of genetic variability (H_o and H_e) in the house mice (*Mus musculus*) per locus and of genetic differentiation (f, θ, and F) among 15 poultry farms based on the analysis of five microsatellite loci.

Locus	n	H_o	H_e	f	θ	F
D1mit122	8	0.64	0.71	0.115**	0.079ns	0.185**
D4mit185	5	0.59	0.63	0.057ns	0.178**	0.225**
D3mit312	4	0.49	0.58	0.123**	0.112**	0.222**
D5mit16	4	0.52	0.55	0.042ns	0.137**	0.172ns
Mmu-2	7	0.54	0.67	0.186**	0.114**	0.279**
Mean		0.56	0.63	0.104**	0.124**	0.216**

Note: n, number of allele per locus; H_o, ~~number of observed heterozygotes~~; H_e, ~~number of expected heterozygotes~~; f, estimate of F_{IS}; θ, estimate of F_{ST}; F, estimate of F_{IT}; **, $p < 0.01$; ns, not significant.

Fig. 2. Genetic distance (F_{ST}) versus geographic distance between populations of house mice (*Mus musculus*) in poultry farms. The correlation index based on the Mantel test is $r = 0.806$, $p = 0.01$.



Discussion

The population of *M. musculus* in the study area is genetically subdivided into groups that differ in terms of the allele frequencies of the studied microsatellites, both among farms and among sheds within farms. These results suggest that movements between farms are limited and that farms are relatively isolated patches of habitat for *M. musculus*. As observed in other systems (Brown 1953; Pocock et al. 2005), this species showed a limited range of movement in farms, which are habitats with high availability of food resources and good microclimatic conditions, compared with the surrounding habitats where interspecific competition with other rodent species may limit both the movements and the establishment of *M. musculus*. Although this species is occasionally captured in sylvan habitats (Kravetz and De Villafañe 1981; Bilenca and Kravetz 1995; Busch et al. 1997, 2001, 2005), the disappearance of *M. musculus* from a poultry farm after it was abandoned and colonized by weeds and native rodents (V.A. León, personal observations) demonstrates the difficulty faced by this species in maintaining stable populations in noncommensal habitats.

The correlation between genetic and geographic distances suggests that most gene flow occurs between neighbouring farms, and that the interchange of individuals is due to active movements and not to passive transport by humans, because this latter mechanism would have diluted genetic differences or would have caused a higher similarity among farms that worked with the same company. A possible mechanism of gene flow between farms could be that of deme extinction and recolonization, a process different from successful incorporation of a migrant within an otherwise stable subpopulation (Dallas et al. 1995), because the territorial behaviour of *M. musculus* limits the successful breeding of alien individuals.

The nonrandom breeding and the genetic differentiation of *M. musculus* among sheds within farms may have been the consequence of limited movements or of territorial behaviour, which occurs in isolated groups with limited interaction between them (Anderson 1970; Berry 1986; Manning et al. 1995). Singleton (1983) observed that even in cases where individuals move between groups, migrants do not significantly contribute to the genetic pool of the group if these groups are socially stable; in cases where groups are unstable, the social structure would not have a long-term effect on genetic flow. In the case of the poultry farms in the study area, groups of *M. musculus* are probably unstable because of high mortality caused by chemical control, and the differentiation between sheds is probably caused by the small range of movements of *M. musculus*, as observed by the tracking with fluorescent powders.

Marked *M. musculus* were never found at the end of the fluorescent track, indicating that our estimates of movements probably correspond to the minimal distances covered by *M. musculus*. The observed values, from 1.55 to 58 m, are similar to the range of values obtained for *M. musculus* in commensal habitats in other countries (Brown 1953; Baker and Petras 1986; Chambers et al. 2000; Pocock et al. 2004; Pocock et al. 2005), and those reported by radio tracking in farms of the study area by ~~D.M.~~ Valenzuela (unpublished data).

According to both direct and indirect estimates of movements, we consider *M. musculus* generally to move short distances, but we cannot dismiss the possibility of dispersal movements over longer distances, which could result in the interchange of individuals and gene flow among farms. The correlation between genetic differentiation and geographic distance suggests that these longer movements do exist, but the method of fluorescent powders and the short sampling period may have prevented their detection.

Our results support our hypothesis 2.1, which states that *M. musculus* move actively among farms, and hence we propose that the unit of control (farms where pest control measures must occur simultaneously) should be the groups of nearby farms, rather than individual farms.

An integrated control program in the study area should also take into account the distances between farms to avoid unsuccessful results because of recolonization. Also, the continuous increase in poultry activity may lead to shorter distances between farms, enhancing the probability of recolonization from neighbour farms.

In summary, we conclude that populations of *M. musculus* in farms of the study area are connected by limited movements and are genetically differentiated, both at a between-farm scale and within farms among different breeding sheds. Furthermore, the magnitude of gene flow depends on the geographic distance, and the unit of control must include groups of nearby farms. Finally, there is no evidence that farms that work with the same company may conduct synchronous control.

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References

Abdelkrim, J., Pascal, M., Calmet, C., and Samadi, S. 2005. Importance of assessing population genetic structure before eradication of invasive species: examples from insular Norway rat populations. Conserv. Biol. **19**(5): 1509–1518. doi:10.1111/j.1523-1739.2005.00206.x.

Acha, P.N., and Szyfres, B. 1992. Zoonosis y enfermedades transmisibles comunes al hombre y a los animales. Organización Panamericana de la Salud, Washington, D.C.

Anderson, P.K. 1964. Lethal alleles in *Mus musculus*: local distribution and evidence for isolation of demes. Science (Washington, D.C.), **145**(3628): 177–178. doi:10.1126/science.145.3628.177. PMID:14171561.

Anderson, P.K. 1970. Ecological structure and gene flow in small mammals. Symp. Zool. Soc. Lond. **26**: 299–325.

Aplin, K.A., and Singleton, G.R. 2003. Balancing rodent management and small mammal conservation in agricultural landscapes: challenges for the present and the future. *In* Rats, mice and people: rodent biology and management. *Edited by* G.R. Singleton, L.A. Hinds, C.J. Krebs, and D.M Spratt. Australian Centre for International Agricultural Research, Canberra. pp. 80–88.

Baker, A.E., and Petras, M.L. 1986. The fate of *Mus domesticus* demes after destruction of their habitats. Biol. J. Linn. Soc. **29**(2): 81–88. doi:10.1111/j.1095-8312.1986.tb01823.x.

Berry, R.J. 1986. Genetics of insular populations of mammals, with particular reference to differentiation and founder effects in British small mammals. Biol. J. Linn. Soc. **28**(1-2): 205–230. doi:10.1111/j.1095-8312.1986.tb01754.x.

Berry, R.J., and Jakobson, M.E. 1974. Vagility in an island population of the house mouse. J. Zool. (1965–1984), **173**(3): 341–354. doi:10.1111/j.1469-7998.1974.tb04119.x.

Bilenca, D.N., and Kravetz, F.O. 1995. Daños a maíz por roedores en la región pampeana (Argentina) y un plan para su control. Vida Silvestre Neotropical (Costa Rica), **4**(1): 51–57.

Bilenca, D.N., Cittadino, E.A., and Kravetz, F.O. 1995. Influencia de la actividad de Cavia aperea sobre la estructura del hábitat y la distribución de *Akodon azarae* y *Oryzomys flavescens* (Rodentia: Caviidae, Muridae) en bordes de cultivos de la región pampeana (Argentina). Iheringia Ser. Zool. **79**: 67–75.

Bonaventura, S.M., and Cagnoni, M.C. 1995. La vegetación de los bordes de caminos en agroecosistemas. Physis, **50**: 63–71.

Brown, R.Z. 1953. Social behaviour, reproduction and population changes in the house mouse (*Mus musculus* L.). Ecol. Monogr. **23**(3): 217–240. doi:10.2307/1943592.

Brown, P. 2005. The effect of simulated house mouse damage to wheat in Australia. Crop Prot. **24**(2): 101–109. doi:10.1016/j.cropro.2004.06.012.

Brown, P., and Singleton, G.R. 2002. Impacts of house mice in crops in Australia — costs and damage. *In* Human conflicts with wildlife: economic considerations. *Edited by* L. Clark, J. Hone, J.A. Shivik, R.A. Watkins, K.C. VerCauteren, and J.K. Yoder. National Wildlife Research Center, Fort Collins, Colo. pp. 48–58.

Busch, M., and Kravetz, F.O. 1992. Competitive interactions among rodents (*Akodon azarae*, *Calomys laucha*, *C. musculinus* and *Oligoryzomys flavescens*) in a two-habitat system. I. Spatial and numerical relationships. Mammalia, **56**(1): 45–56. doi:10.1515/mamm.1992.56.1.45.

Busch, M., Alvarez, M.R., Cittadino, E.A., and Kravetz, F.O. 1997. Habitat selection and interspecific competition in rodents in pampean agroecosystem. Mammalia, **61**(2): 167–184. doi:10.1515/mamm.1997.61.2.167.

Busch, M., Mino, M., Dadon, J., and Hodara, K. 2001. Habitat selection by *Akodon azarae* and *Calomys laucha* (Rodentia, Muridae) in pampean agroecosystems. Mammalia, **65**(1): 29–48. doi:10.1515/mamm.2001.65.1.29.

Busch, M., Bilenca, D.N., Cittadino, E.A., and Cueto, G. 2005. Effect of removing a dominant competitor, *Akodon azarae* (Rodentia, Sigmodontinae) on community and population parameters of small rodent species in Central Argentina. Austral Ecol. **30**(2): 168–178. doi:10.1111/j.1442-9993.2004.01434.x.

Chambers, L.K., Singleton, G.R., and Krebs, C.J. 2000. Movements and social organization of wild house mice (*Mus domesticus*) in the wheatlands of northwestern Victoria, Australia. J. Mammal. **81**(1): 59–69. doi:10.1644/1545-1542(2000)081<0059:MASOOW>2.0.CO;2.

Cochran, W.W., and Lord, R.D., Jr. 1963. A radio-tracking system for wild animals. J. Wildl. Manage. **27**(1): 9–24. doi:10.2307/3797775.

Dallas, J.F., Dod, B., Bourso, P., Prager, E.M., and Bonhomme, F. 1995. Population subdivision and gene flow in Danish house mice. Mol. Ecol. **4**(3): 311–320. doi:10.1111/j.1365-294X.1995.tb00224.x. PMID:7663750.

Drickamer, L.C., Feldhamer, G.A., Mikesic, D.G., and Holmes, C.M. 1999. Trap-response heterogeneity of house mice (*Mus musculus*) in outdoor enclosures. J. Mammal. **80**(2): 410–420. doi:10.2307/1383289.

Elias, D.J. 1988. Overview of rodent problem in developing countries. FAO Bol. Fitosanit. **36**: 107–110.

Goudet, J. 2002. FSTAT: a program to estimate and test gene diversities and fixation indices. Version 2.9.3.2 [computer program]. Available from http://www2.unil.ch/popgen/softwares/fstat.htm [accessed May 2006].

Hanski, I.A., and Gilpin, M.E. 1997. Metapopulation biology: ecology, genetics and evolution. Academic Press, San Diego, Calif.

Hayne, D.W. 1949. Calculation of size of home range. J. Mammal. **30**(1): 1–18. doi:10.2307/1375189.

Jacob, J., Ylönen, H., Runcie, M.J., Jones, D.A., and Singleton, G.R. 2003. What affects bait uptake by house mice in Australian grain fields? J. Wildl. Manage. **67**(2): 341–351. doi:10.2307/3802776.

Jike, L., Batzli, G.O., and Getz, L.L. 1988. Home ranges of prairie voles as determined by radiotracking and by powdertracking. J. Mammal. **69**(1): 183–186. doi:10.2307/1381772.

Kravetz, F., and De Villafañe, G. 1981. Poblaciones de roedores en cultivo de maíz durante las etapas de madurez y rastrojo. Hist. Nat. **1**(31): 213–232.

Kravetz, F., Bellocq, M., Busch, M., Bonaventura, S.M., and Monjeau, A. 1987. Efecto de la aplicación de un anticoagulante sobre la comunidad de roedores en campos de cultivo. An. Mus. Hist. Nat. Valparaíso, **18**: 153–156.

Lemen, C.A., and Freeman, P.W. 1985. Tracking mammals with fluorescent pigments: a new technique. J. Mammal. **66**(1): 134–136. doi:10.2307/1380966.

León, V., Guidobono, J.S., and Busch, M. 2007. Abundancia de *Mus domesticus* en granjas avícolas, efectos locales vs. efectos espaciales. Ecol. Austral, **17**: 189–198.

Levitan, D.R., and Grosberg, R.K. 1993. The analysis of paternity and maternity in the marine hydrozoan *Hydractinia symbiolongicarpus* using randomly amplified polymorphic DNA (RAPD) markers. Mol. Ecol. **2**(5): 315–326. doi:10.1111/j.1365-294X.1993.tb00024.x. PMID:7909258.

Manning, C.J., Dewsbury, D.A., Wakeland, E.K., and Potts, W.K. 1995. Communal nesting and communal nursing in house mice, *Mus musculus domesticus*. Anim. Behav. **50**(3): 741–751. doi:10.1016/0003-3472(95)80134-0.

Mikesic, D.G., and Drickamer, L.C. 1992. Factors affecting home-range size in house mice (Mus musculus domesticus) living in outdoor enclosures. Am. Midl. Nat. **127**(1): 31–40. doi:10.2307/2426319.

Miller, M.P. 2000. Tools for population genetic analyses (TFPGA): a Windows program for the analyses of allozyme and molecular population genetic data. Version 1.3 [computer program]. Available from http://www.marksgeneticsoftware.net/ [accessed May 2006].

Mills, J.N., Ellis, B., Mckee, K., Maiztegui, J., and Childs, J.E. 1991. Habitat associations and relative densities of rodent population in cultivated areas of Central Argentina. J. Mammal. **72**(3): 470–479. doi:10.2307/1382129.

Miño, M.H., Cavia, R., Gómez Villafañe, I.E., Bilenca, D.N., Cittadino, E.A., and Busch, M. 2001. Estructura y diversidad de dos comunidades de pequeños roedores en agroecosistemas de la provincia de Buenos Aires, Argentina. Bol. Soc. Biol. Concepcion, **72**: 67–75.

Miño, M.H., Cavia, R., Villafañe, I.G., Bilenca, D.N., and Busch, M. 2007. Seasonal abundance and distribution among habitats of small rodents on poultry farms. A contribution for their control. Int. J. Pest Manage. **53**(4): 311–316. doi:10.1080/09670870601105949.

Moritz, C., Worthington Wilmer, J., Pope, L., Sherwin, W.B., Taylor, A.C., and Limpus, C.J. 1996. Applications of genetics to the conservation and management of Australian fauna: four case studies from Queensland. *In* Molecular genetics approaches to conservation. *Edited by* T.B. Smith and R.K. Wayne. Oxford University Press. New York pp. 442–456.

Myers, J.H. 1974. Genetic and social structure of feral house mouse populations on Grizzly Island, California. Ecology, **55**(4): 747–759. doi:10.2307/1934411.

Nicolas, V., and Colyn, M. 2007. Efficiency of fluorescent powder tracking for studying use of space by small mammals in an African rainforest. Afr. J. Ecol. **45**(4): 577–580. doi:10.1111/j.1365-2028.2007.00771.x.

Pocock, M.J.O., Searle, J.B., and White, P.C.L. 2004. Adaptations of animals to commensal habitats: population dynamics of house mice *Mus musculus domesticus* on farms. J. Anim. Ecol. **73**(5): 878–888. doi:10.1111/j.0021-8790.2004.00863.x.

Pocock, M.J.O., Hauffe, H., and Searle, J.B. 2005. Dispersal in house mice. Biol. J. Linn. Soc. **84**(3): 565–583. doi:10.1111/j.1095-8312.2005.00455.x.

Reimer, J.D., and Petras, M.L. 1967. Breeding structure of the house mouse, *Mus musculus*, in a population cage. J. Mammal. **48**(1): 88–99. doi:10.2307/1378173. PMID:6045185.

Ritche, M.E. 1997. Populations in a landscape context: sources, sinks and metapopulations. *In* Wildilife and landscape ecology. Effects of pattern and scale. *Edited by* J.A. Bissonette. Springer-Verlag. New York. pp. 160–184.

Robertson, B.C., and Gemmel, N.J. 2004. Defining eradication units to control invasive pests. J. Appl. Ecol. **41**(6): 1042–1048. doi:10.1111/j.0021-8901.2004.00984.x.

Rousset, F., and Raymond, M. 1995. Testing heterozygote excess and deficiency. Genetics, **140**(4): 1413–1419. PMID:7498780.

Ryan, A.W., Duke, E.J., and Fairley, J.S. 1993. Polymorphism, localization and geographical transfer of mitochondrial DNA in *Mus musculus domesticus* (Irish house mice). Heredity, **70**(1): 75–81. doi:10.1038/hdy.1993.11. PMID:8094386.

Selander, R.K. 1970. Behavior and genetic variation in natural populations. Am. Zool. **10**(1): 53–66. PMID:5437297.

Shaw, P.W., Turan, C., Wright, J.M., O'Connell, M., and Carvalho, G.R. 1999. Microsatellite DNA analysis of population structure in Atlantic herring (*Clupea harengus*), with direct comparison to allozyme and mtDNA RFLP analyses. Heredity, **83**(4): 490–499. doi:10.1038/sj.hdy.6885860. PMID:10583552.

Singleton, G.R. 1983. The social and genetic structure of a natural colony of house mice, *Mus musculus*, at Healesville Wildlife Sanctuary. Aust. J. Zool. **31**(2): 155–166. doi:10.1071/ZO9830155.

Singleton, G.R., and Hay, D.A. 1983. The effect of social organization on reproductive success and gene flow in colonies of wild house mice, *Mus musculus*. Behav. Ecol. Sociobiol. **12**(1): 49–56. doi:10.1007/BF00296932.

Singleton, G.R., Sudarmaji, Jacob, J., and Krebs, C.J. 2005. Integrated management to reduce rodent damage to lowland rice crops in Indonesia. Agric. Ecosyst. Environ. **107**(1): 75–82. doi:10.1016/j.agee.2004.09.010.

Smith, R.H. 1994. Rodent control methods: non-chemical and non-letal chemical. *In* Rodent pests and their control. *Edited by* A.P. Buckle and R.H. Smith. CAB International, Wallingford, Oxfordshire, UK. pp. 109–125.

Timm, R.M. 1994. House mice. *In* Prevention and control of wildlife damage. *Edited by* S.E. Hygnstrom, R.M. Timm, and G.E. Larson. University of Nebraska Cooperative Extension, Lincoln. pp. 31–46.

Weir, B., and Cockerham, C.C. 1984. Estimating *F*-statistics for the analysis of population structure. Evolution, **38**(6): 1358–1370. doi:10.2307/2408641.

Wright, S. 1943. Isolation by distance. Genetics, **28**(2): 114–138. PMID:17247074.

Wright, S. 1965. The interpretation of population structure by *F*-statistics with special regard to systems of mating. Evolution, **19**(3): 395–420. doi:10.2307/2406450.

Wright, S. 1978. Variability within and among natural populations in evolution and the genetics of populations. University of Chicago Press, Chicago.

Zhang, M., Wang, Y., and Li, B. 2003. Changes in community composition and population dynamics of commensal rodents in farmhouses in the Dongting Lake region of China. *In* Rats, mice and people: rodent biology and management. *Edited by* G.R. Singleton, L.A. Hinds, C.J. Krebs, and D.M. Spratt. Australian Centre for International Agricultural Research, Canberra. pp. 256–259.