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# Spatio-temporal genetic structure of the rodent *Calomys venustus* in linear, fragmented habitats

Marina B. Chiappero,* Lucía V. Sommaro, José W. Priotto, María Paula Wiernes, Andrea R. Steinmann, and Cristina N. Gardenal

*Instituto de Diversidad y Ecología Animal. Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET) and Universidad Nacional de Córdoba, Av. Vélez Sarsfield 299, X5000JJC Córdoba, Argentina (MBC, LVS, MPW, CNG)*
*Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), and Grupo de Investigaciones en Ecología Poblacional y Comportamental (GIEPCO),Universidad Nacional de Río Cuarto, Ruta 36 Km 601, X5804BYA Río Cuarto, Argentina (JWP, ARS)*

* *Correspondent: mchiappero@efn.unc.edu.ar*

Studies about habitat fragmentation, in terms of how it affects gene flow and genetic variability, have traditionally been conducted on island-like systems in which the remaining habitats form patches embedded in a matrix. However, in agroecosystems, remaining habitats usually form linear strips along fence lines, roads, and water courses ("border" habitats). We used the rodent *Calomys venustus*, a species inhabiting borders in central Argentina agroecosystems, as a model to address how genetic variability is structured in linear habitats. A total of 359 rodents were captured seasonally from spring 2005 to winter 2006. Genetic variability at microsatellite loci was uniformly high, despite significant variation in population size during the sampling period. Genetic differentiation, spatial autocorrelation, and causal modeling analyses suggested that dispersion patterns in this species depend mainly on geographic distance, with unfavorable habitat like dirt roads and crop fields posing only weak (or no) resistance to dispersal. Small-scale spatial genetic structure was related to different space use patterns by females and males. Our results showed that, although greatly reduced in area, border habitats can support stable populations of species without loss of either variability or genetic connectivity.

Los efectos de la fragmentación del hábitat sobre el flujo génico y la variabilidad genética, se han estudiado tradicionalmente en sistemas tipo islas, en los cuales los hábitats remanentes forman parches embebidos en una matriz. Sin embargo, en los agroecosistemas, éstos suelen tener forma lineal a lo largo de alambrados, caminos y corrientes de agua (hábitats de "borde"). En este trabajo, utilizamos al roedor *Calomys venustus*, especie típica de ambientes de borde en los agroecosistemas del centro de Argentina, como modelo para estudiar cómo la variabilidad genética se estructura en hábitats lineales. Un total de 359 roedores se capturaron estacionalmente desde la primavera de 2005 hasta el invierno de 2006. La variabilidad genética encontrada en loci de microsatélites fue siempre alta, a pesar de una variación significativa del tamaño poblacional a lo largo del período de estudio. Los análisis de diferenciación genética, autocorrelación genética espacial y modelado causal sugieren que los patrones de dispersión en esta especie dependen principalmente de la distancia geográfica, y que los hábitats desfavorables como caminos de tierra y campos de cultivo representan una barrera débil (o nula) para la dispersión. La estructura genética a escala pequeña estuvo relacionada al diferente uso del espacio por parte de machos y hembras. Nuestros resultados mostraron que a pesar de tener un área reducida, los hábitat de bordes pueden mantener poblaciones estables sin pérdida de variabilidad genética o reducción del flujo génico.

Key words: agroecosystem, *Calomys venustus*, dispersal, genetic structure, linear habitat, maintenance of genetic variability, microsatellite, spatial genetic autocorrelation





The expansion of agricultural land worldwide has exacerbated the loss of natural habitats, transforming the landscape into remnant patches of natural areas separated by croplands. Immediate consequences for animal populations are a decrease in the amount of available habitat and increased isolation, which can reduce or even interrupt dispersal and therefore gene flow among formerly connected populations (Fahrig 2003; Fischer and Lindenmayer 2007). Isolated populations are more

susceptible to the effects of genetic drift causing loss of genetic diversity and inbreeding, which in turn can affect the ability of populations to cope with environmental challenges, increasing their probability of extinction. Further, isolated patches are less likely to be recolonized from other patches (Spielman et al. 2004; Frankham 2005; Garner et al. 2005). Both descriptive and experimental studies in small mammals reveal that the extent to which landscape modification results in isolation and decreased gene flow depends on several environmental- and species-specific factors including the particular way in which the landscape has been modified, the presence of corridors among fragments providing means for dispersal, mode and scale of movement, and dispersal behavior (Rosenberg et al. 1997; Aars et al. 1998; Aars and Ims 1999; Andreassen and Ims 2001; Mabry and Barrett 2002; Pardini et al. 2005; Fahrig 2007; Fischer and Lindenmayer 2007; Rémy et al. 2011). For example, fragmentation would affect mainly the dispersing sex (Banks et al. 2005; Walker et al. 2008) or affect habitat specialists more than generalists, either because the latter would be more tolerant to the low quality of the matrix and therefore would be able to move more efficiently through it (Mabry and Barrett 2002) or because they are more prone to make use of habitat corridors among patches (Mech and Hallett 2001; McDonald and St Clair 2004). Most of these studies deal with the analysis of "island-like" systems in which the original, continuous habitat of a species is transformed into a number of smaller patches, isolated from each other by a matrix of modified habitats. However, this approach may be inappropriate in agroecosystems, where original habitats often remain as narrow strips along fences, water courses, roads, and railways and therefore have an essentially linear instead of a 2-dimensional shape.

In Argentina, the extensive plains that occupy approximately 500,000 km$^2$ in the central part of its territory provide most of the country's agricultural production. Therefore, this area has suffered the highest degree of alteration of any region in the country. In a process that accelerated during the 2nd half of the 20th century, the original prairies were almost completely replaced by agricultural plots and livestock pastures. Only small and geographically marginal areas, unsuitable for agriculture, remain in a relatively natural state (Krapovickas and di Giacomo 1998; Manuel-Navarrete et al. 2005; Demaría et al. 2008). The remnant habitats that are most similar to original habitats are narrow strips along fence lines separating crop and pasture fields, water streams, roads, and railroads, where a mixed community of native and introduced plants persists. Even for small mammals, these "border" habitats have a linear instead of a 2-dimensional structure. Their average width is 2 m (although some borders along railroads and water currents can be as wide as 50 m) and can go uninterrupted for several kilometers (Crespo 1966; Crespo et al. 1970; Ellis et al. 1997; Sommaro et al. 2010; Gomez et al. 2011). Traditionally, the study of linear habitats in the context of fragmentation has focused on their role as corridors linking patches of suitable habitat (Bennett 1990; Rosenberg et al. 1997; Puth and Wilson 2001). However, they also may contain resources for long-term survival and reproduction, and in some cases, they are the only available habitat for wild animal species (Fauske et al. 1997; Gelling et al. 2007) as is the case in central Argentina. Here, borders harbor an assemblage of small mammals dominated by rodents of the subfamily Sigmodontinae. The species *Calomys venustus* is one of the most abundant and shows a strong preference for habitats with high vegetation cover. In agroecosystems, this requirement is best fulfilled by borders, and therefore this species is usually confined to these habitats (Simone et al. 2010). The reproductive season of this species spans from the end of winter or beginning of spring (August–September) to the beginning of autumn (March–April—Priotto et al. 2002). Population density increases during the breeding period, with a peak in autumn followed by a sharp decline in winter (Polop et al. 2005). The species is characterized by a promiscuous-polygynous mating system. Home range sizes are similar in both sexes but are larger during the breeding period and at low population densities. Males and females use space differently in the breeding and non-breeding periods. During breeding, females keep exclusive home ranges, while in the non-breeding period they share their home range with other females. Males, on the contrary, share their home ranges with both sexes throughout the year (Priotto et al. 2002). Males of this species move longer distances than females in border habitats, and both sexes show a negative relationship between abundance and movement. Recorded movement distances are in general short (less than 40 m), but a small number of individuals move long distances (up to 1,650 m) and even cross dirt roads (Gomez et al. 2011).

In this work, we used *C. venustus* as a model organism to explore how genetic variability is structured spatially and temporally in linear habitats, such as those commonly found in agricultural ecosystems worldwide. Having a strong preference for tall vegetation and being confined to border habitats, our main hypothesis was that roads and crop fields separating different borders would constitute barriers for dispersal, and that each border would harbor small, essentially isolated populations with low levels of genetic variability as a result of genetic drift being weakly counterbalanced by gene flow. Dispersal differs between sexes and with abundance, so we also tested the hypothesis that females are more genetically structured at small spatial scales than males, and that structure is inversely related to abundance.

## Material and Methods

*Study area and sample collection.*—Sampling was carried out in linear habitats of an agriculture ecosystem in Río Cuarto Department (Córdoba Province, Argentina). The landscape consists of crop fields, surrounded by wire fences and crossed by paved or dirt roads and by water courses, along which border habitats can be found. Four sampling transects were set up on opposite sides of two 7-m-wide secondary dirt roads perpendicular to each other and 4.5 km away: transect A opposite to transect B, and C opposite to D (Fig. 1). Sherman-like live traps were used to capture rodents; each trap was georeferenced using a Garmin eTrex Legend GPS receiver (Garmin Corporation, Olathe, Kansas).

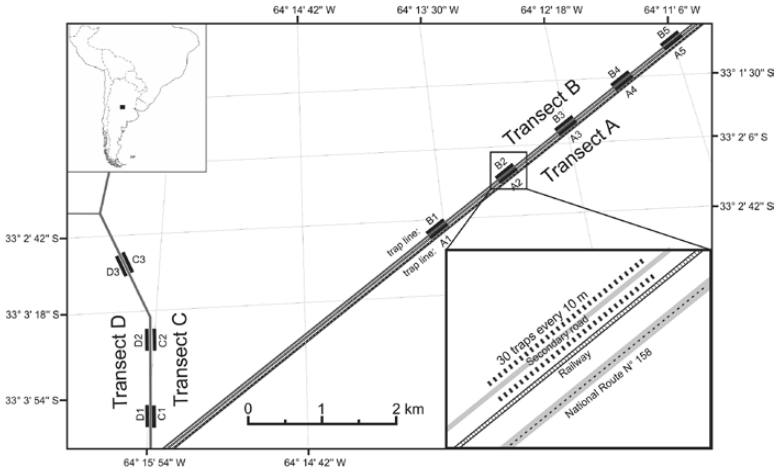


**Fig. 1.**—Map of the sampling design, located in linear habitats of an agriculture ecosystem in Río Cuarto Department (Córdoba Province, Argentina).

We conducted 4 seasonal capture, mark, and recapture (CMR) trapping sessions, 5 days long each, in November 2005 (Spring, beginning of the breeding period, low population density), March 2006 (end of Summer and of the breeding period, intermediate population density), May 2006 (Autumn, beginning of the non-breeding period, high population density), and July 2006 (Winter, non-breeding period, low population density). Trapped animals were sexed, weighed, measured (body and tail length), and ear-tagged. Reproductive condition (males: scrotal or abdominal testicles; females: perforated or imperforated vulva, pregnancy evidence, visible nipples or not) was also recorded. Individuals were classified as juveniles or adults following Priotto (2000). A small piece of the tail tip was cut and preserved in 90% ethanol for microsatellite genotyping. Field procedures conformed to national guidelines of the Argentine National Council for Scientific and Technological Research (CONICET) as well as those of the American Society of Mammalogists (Sikes et al. 2011).

*Microsatellite genotyping.*—Genomic DNA was extracted from tail tips using the DirectPCR (Tail) kit (Viagen-Biotech Inc., Los Angeles, California) following manufacturer's instructions. Primers for 10 microsatellite loci, developed for the syntopic species *C. musculinus* (Chiappero et al. 2005, 2011), were assayed. In initial test panels, loci amplified successfully; however, loci Cmu2, Cmu4, Cmu13, and Cmu15 were monomorphic. The remaining 6 loci were used in this study (Supporting Information S1).

Polymerase chain reactions were performed using a Biometra TPersonal thermocycler (Biometra, Göttingen, Germany). Reactions were set in a final volume of 10 µl, containing 0.5 unit of Taq polymerase (Fermentas, Burlington, Canada), 5 ng of genomic DNA, 1.25–2.0 mM $MgCl_2$ according to primer (Supporting Information S1), 0.4 µM of each primer, 60 µM of each dNTP (GE Healthcare, Uppsala, Sweden), and 1.3 M of Betaine (Sigma-Aldrich, St. Louis, Missouri). The cycling program for all loci consisted of an initial denaturation step at 92° C for 5 min, followed by 32 cycles of denaturation at 92° C for 30 s, 30 s at the annealing temperature (Supporting Information S1), and extension at 72° C for 30 s; the final extension step consisted of 5 min at 72° C.

Loci Cmu6 and Cmu11 were observed to be diagnostic loci differentiating *C. venustus* from *C. musculinus* (Sommaro 2012). Since juveniles of both species can be easily confounded (Massoia and Fornes 1965), we first amplified all samples for these 2 loci to avoid including individuals of other species in our database. Alleles of these loci were separated by electrophoresis on 8% native polyacrylamide vertical gels using the tris glycine buffer system (White et al. 2002) and stained with silver nitrate (Neilan et al. 1994). Allele sizes were inferred by comparison to a molecular size standard (10 bp DNA Ladder; Invitrogen, Carlsbad, California). Amplification of loci Cmu1, Cmu3, Cmu14, and Cmu17 was performed using fluorescently labeled forward primers and the molecular size of the amplification products was determined using an ABI3100 sequencer at Macrogen Inc (Seoul, Korea). Fragments were scored using the software PeakScanner v1.0 (Applied Biosystems, Foster City, California) and binned using MsatAllele package v1.05 in R 3.0.1 (Alberto 2009; R Development Core Team 2013), which defines the bin limits based on the distribution properties of the observed fragment sizes.

*Data analysis.*—Each season was checked for the presence of null alleles and scoring errors due to stuttering or to large allele drop outs using the program Microchecker (van Oosterhout et al. 2004). We assessed conformance to Hardy–Weinberg equilibrium by locus, transect, and season using the index *f*, the correlation between alleles within individuals within populations (analogous to Wright's $F_{IS}$) using FSTAT v2.9.3.2 (Goudet 2001). Significance levels for *f* were calculated by 24,000 randomizations of alleles among individuals within samples and adjusted using the sequential Bonferroni correction for multiple tests (Rice 1989).

Genetic variability was measured by season as mean allelic richness (AR), in which genotype data are resampled to give sample sizes equal to the smallest sample size and as mean expected heterozygosity ($H_e$) using FSTAT. The significance of differences in levels of genetic variability among seasons

was assessed through a Friedman test with the program Infostat (Balzarini et al. 2008).

We explored the genetic differentiation within each season using population- and individual-based approaches. The genetic differentiation between transects set along different secondary roads (A + B versus C + D) and between transects on opposite sides of the same road was estimated using the standardized measure of population differentiation $G'_{ST}$ (Hedrick 2005) to account for the high intrapopulation variability, using the R program DiveRsity (Keenan 2012). Ninety-five percent confidence intervals (95% *CI*s) were constructed by means of 1,000 bootstrap replications to estimate statistical significance of $G'_{ST}$ values.

The spatial pattern of genetic variation (spatial genetic structure—SGS) was determined on the basis of individual multilocus genotypes using 2 approaches. First, spatial autocorrelation analyses were performed for the total population by season, by season and sex, and by season and transect with Genalex 6.5 (Peakall and Smouse 2006). Starting from pairwise geographical and genetic distance matrices, this approach calculates a multivariate autocorrelation coefficient, *r*, that measures the genetic similarity of pairs of individuals whose geographical separation falls within a given distance class. The coefficient *r* is bounded by [−1, +1] with a mean of 0 when pairs of individuals within a distance class are as similar genetically as expected by chance. A significantly positive *r* indicates that individuals within that distance class are genetically more similar than expected by chance. A significantly negative *r* indicates no dependence among genotypes at the spatial scale considered, as a result of restricted gene flow at that scale. Spatial autocorrelation analyses were performed using the Multiple Dclass option in Genalex, which estimates the extent of spatial autocorrelation as a function of cumulative geographical distance. The distance classes at which autocorrelation coefficients no longer remained significant are considered to be an approximation of the extent of significant genetic structure (Peakall et al. 2003). Distance classes were chosen in order to include an intratrap line component (100, 200, and 300 m) and an intertrap line component (starting from 1,100 m in 800-m intervals), which were set using the "variable distance classes" option. Tests of statistical significance of *r* values were performed according to Peakall et al. (2003). The 95% *CI* around the null hypothesis of no genetic structure ($r = 0$) was determined by 10,000 random permutations of genotypes among geographic locations. Additionally, the 95% *CI* about each value of *r* was obtained by 10,000 bootstrap resamplings within each distance class; however, it should be kept in mind that this test is more conservative than permutational tests and will therefore favor the null hypothesis of no autocorrelation more frequently than permutational tests (Peakall et al. 2003).

Second, we evaluated the effect of geographic distance and of different elements of the landscape (borders, crop fields, secondary roads) on genetic differentiation between *C. venustus* individuals using partial Mantel tests and a causal modeling approach (Cushman et al. 2006; McRae et al. 2008; Cushman and Landguth 2010). We generated resistance maps of the study site, representing different hypotheses about the difficulty of *C. venustus* individuals to disperse through different landscape elements. Maps were drawn at the scale 1:1,250 from a Google Earth image using the OpenLayer plugin within QGIS 2.6.1 (QGIS Development Team 2014). The elements of the landscape were classified into 3 classes, secondary roads, crop/pasture fields, and borders, and assigned a resistance value representing the cost to movement for *C. venustus*. Five hypotheses about connectivity in the agroecosystem were generated (Table 1). Borders were assigned the minimum resistance in all models, due to the strong preference of the species for tall vegetation. Fields and secondary roads were assigned alternatively high and low resistance values (Table 1), to generate a total of 4 isolation by resistance (IBR) hypotheses. Finally, the last model (null model) considered only Euclidean distance as a factor. We used Circuitscape 4.0 (McRae et al. 2014) to transform resistance maps into resistance distance matrices between pairs of individuals using a 4 neighbor connection scheme. Genetic distances between individuals were estimated using the shared allele distance (*Dps* = (1 - proportion of shared alleles at all loci)/number of loci) with the program MSANALIZER 4.05 (Dieringer and Schlötterer 2003). *Dps* was found to properly reflect genetic patterns at the fine-scale level (Keller et al. 2013). First, we conducted simple Mantel tests between *Dps* and each of the distance matrices (null and landscape resistance hypotheses 1 to 4; Table 1). Second, we performed partial Mantel tests between *Dps* and each landscape resistance hypothesis, partialling out the effects of geographic distance. Finally, we performed partial Mantel tests between *Dps* and geographic distance, partialling out the effects of significant resistance hypotheses. If a particular hypothesis of landscape resistance affects gene flow, we expect a simple Mantel test between *Dps* and the particular hypothesis to be significant; partial Mantel tests between *Dps* and the hypothesis, partialling out the effect of geographic distance, to be significant too; and partial Mantel tests between *Dps* and geographic distance,

**Table 1.**—Hypotheses about landscape resistance to gene flow in *Calomys venustus* and resistance values assigned to landscape elements.

| Hypothesis | | Borders | Crop/pasture field | Secondary roads |
|---|---|---|---|---|
| 1 | Fields and secondary roads show high resistance to gene flow | 1 | 50 | 50 |
| 2 | Fields and secondary roads show low resistance to gene flow | 1 | 10 | 10 |
| 3 | Fields show low resistance to gene flow; secondary roads show high resistance to gene flow | 1 | 10 | 50 |
| 4 | Fields show high resistance to gene flow; secondary roads show low resistance to gene flow | 1 | 50 | 10 |
| Null | All habitat types show no resistance to gene flow | 1 | 1 | 1 |

partialling out the effect of the resistance hypothesis, to be non-significant (Cushman et al. 2006). We used the program zt (Bonnet and van de Peer 2002) for all Mantel tests.

## Results

We captured a total of 359 unique individuals: 44 were obtained in spring, 91 in summer, 182 in autumn, and 42 in winter (Supporting Information S2). Most individuals were trapped in transects A and B, while transects C and D accounted for a small part of captures in all seasons. The sex ratio (males/females) was 1 in spring, 0.89 in summer, 1.34 in autumn, and 2.63 in winter.

*Genetic variability.*—Data analysis using Microchecker revealed no genotyping errors or null alleles. Seasonal *f* values showed a small heterozygosity deficit (Supporting Information S3). Levels of genetic variability were high (Table 2) and showed no significant differences among seasons (Friedman test $P = 0.491$ for $H_e$ and $P = 0.194$ for AR).

*Genetic differentiation.*—Significant differentiation was found between the 2 groups of transects (A + B versus C + D) in spring, summer, and autumn (Table 3). Differentiation between transects on opposite sides of the same road was calculated only for Transects A and B, since C and D yielded very low captures in all seasons, and was non-significant in any season (Table 3).

*Spatial autocorrelation analyses.*—The spatial genetic autocorrelation analyses detected significant genetic structuring from the beginning of the breeding period to the beginning of the non-breeding period (Figs. 2a–c). The maximum spatial extent of positive structure was very small at the beginning of the breeding period (100 m in spring, Fig. 2a) and increased considerably toward its end and the beginning of the non-breeding period (1,900 m; Figs. 2b and 2c). There was no detectable spatial genetic structure in winter (Fig. 2d). The low capture success in spring and winter would decrease our power to detect positive structure in these seasons. However, given that capture effort was the same in all seasons, lower captures would result from a real decrease in population sizes; distribution of genotypes of surviving and overwintering individuals would be random.

Spatial autocorrelation analyses by sex are shown in Fig. 3. We do not report results from winter since all analyses yielded a random SGS with low *r* values for all distance classes. In spring, males presented one of the highest *r* values registered in the whole study ($r = 0.065$; Fig. 3a); however, this value was non significant. This outcome would result from the low power of permutation and bootstrap tests due to the low size of this sample ($N = 22$). In summer, males showed a patchy SGS. A significant positive structure was found when considering males between 0–1,100 m and 0–1,900 m. In autumn, they presented a random pattern. Females showed no structuring in spring and in summer. On the contrary, positive structure was strong and extended to a maximum of 1,100 m in autumn (Fig. 3). Analyses by transect were performed only for transects A and B (Fig. 4). Both transects showed contrasting autocorrelation patterns in spring and summer. In spring, transect B presented positive structure until 300 m, while transect A showed a random pattern of genotype distribution. In summer, transect B showed a random pattern, while autocorrelation extended until 200 m in transect A. In autumn, both transects showed significant positive autocorrelation until 300 m.

*Landscape resistance to gene flow.*—Simple Mantel tests between genetic distance and geographic distances or resistance hypotheses were non-significant in spring and winter (Supporting Information S4). On the contrary, we observed significant correlation of genetic distance with all 5 hypotheses in summer and autumn (Supporting Information S4). However, we found significant effects of landscape elements on the genetic differentiation between individuals only in summer: partial Mantel test between *Dps* and Hypothesis 2 (partialling out geographic distance) was significant, while that between *Dps* and geographic distance partialling out Hypothesis 2 was not (Supporting Information S4). This hypothesis proposed that crop/pasture fields and secondary roads exert a low resistance to gene flow. In autumn, genetic differentiation among individuals was best explained by geographic distance alone.

**Table 2.**—Levels of genetic variability in *Calomys venustus* by season. $H_e$: mean expected heterozygosity; AR: mean allelic richness; *SD*: standard deviation.

| | $H_e$ (*SD*) | AR (*SD*) |
|---|---|---|
| Spring | 0.732 (0.213) | 7.856[a] (3.168) |
| Summer | 0.691 (0.268) | 8.013[a] (3.067) |
| Autumn | 0.687 (0.269) | 7.543[a] (2.874) |
| Winter | 0.699 (0.275) | 8.440[a] (3.187) |

[a] Based on a minimum sample size of 38 diploid individuals.

**Table 3.**—Genetic differentiation ($G'_{ST}$) between transects set on both sides of different secondary roads (A + B versus C + D) and on both sides of the same secondary road (A versus B). Bias corrected 95% confidence limits around $G'_{ST}$ were calculated through 1,000 bootstrap replicates and are indicated in parenthesis.

| Season | A + B versus C + D | A versus B |
|---|---|---|
| Spring | 0.150 (0.037 to 0.312) | 0.049 (–0.036 to 0.156) |
| Summer | 0.049 (0 to 0.125) | 0.005 (–0.026 to 0.046) |
| Autumn | 0.056 (0.014 to 0.111) | 0.010 (–0.007 to 0.032) |
| Winter | 0.042 (–0.027 to 0.165) | –0.006 (–0.083 to 0.100) |

## Discussion

Field and experimental work has established that a common consequence of fragmentation is a reduction, or even interruption, of dispersal among formerly connected populations. Therefore, isolated populations will typically experience a loss of genetic variability because genetic drift is no longer counteracted by gene flow (Fahrig 2003; Fischer and Lindenmayer 2007; Chiappero et al. 2011). In this work, we studied the spatial genetic structure of *C. venustus* in border habitats of an agricultural ecosystem, where fragmentation produces linear habitats of few meters width and several kilometers long,

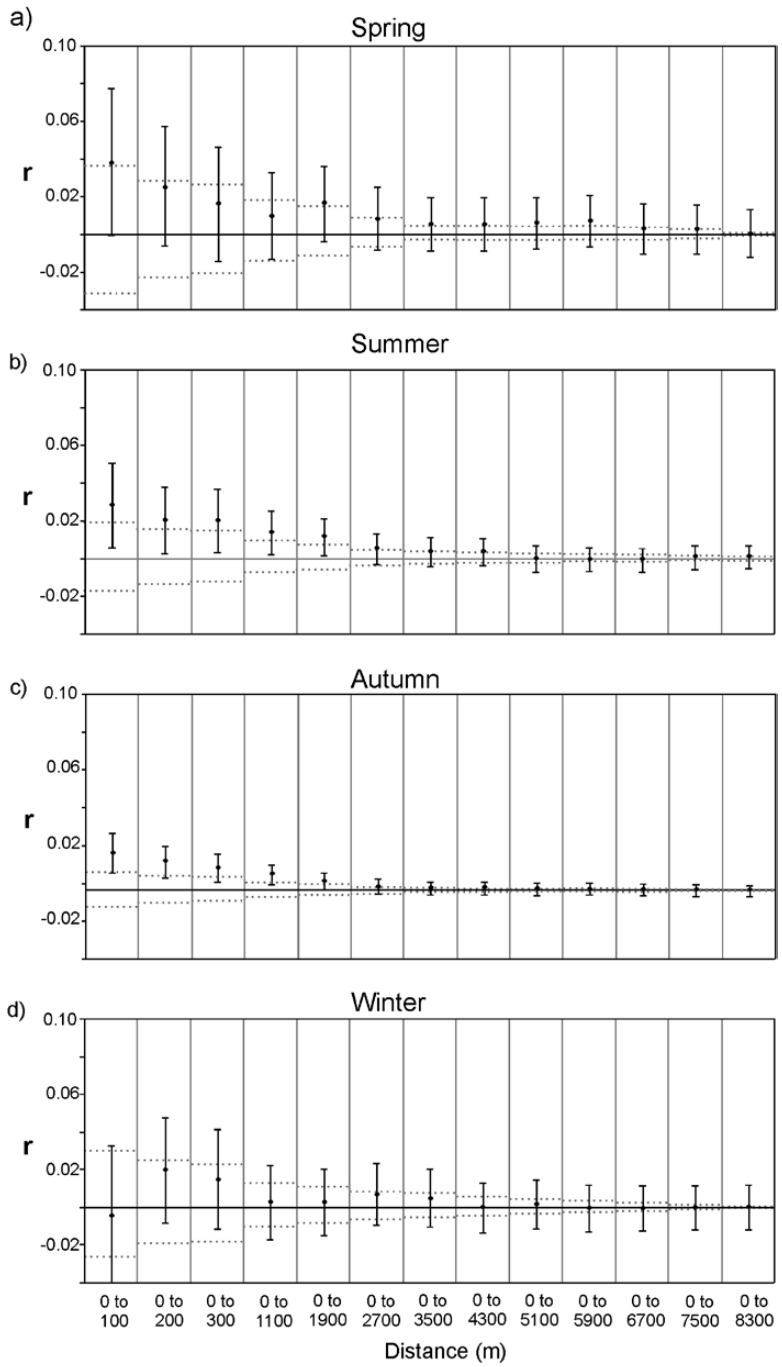


**Fig. 2.**—Seasonal spatial autocorrelation analyses of *Calomys venustus*. a) Spring (November 2005, beginning of the breeding period); b) summer (March 2006, ending of the breeding period); c) autumn (May 2006, beginning of the non-breeding period); d) winter (July 2006, non-breeding period). The grey dotted line indicates the upper and lower bounds of the 95% confidence interval (*CI*) around the null hypothesis of no spatial structure ($r = 0$). The vertical bars indicate the 95% *CI* around each observed value of $r$.

instead of the usual form of island-like patches of original habitats distributed in a matrix of unsuitable habitats.

In this study, population abundance in *C. venustus* rose from a minimum in winter and spring to a post-reproductive peak in autumn (Gomez et al. 2011) as was observed in previous studies (Polop et al. 2005). These changes are accompanied by a rapid population turnover (Priotto 2000; Polop et al. 2005): at the beginning of the breeding period in spring, overwintering animals produce the 1st cohort. During summer, the 1st cohort and surviving overwintering rodents produce the 2nd cohort. At the beginning of autumn, overwintering and 1st cohort animals are no longer trapped, and animals from the 2nd cohort produce the 3rd one. The 2nd and 3rd cohorts provide the overwintering rodents of the next breeding period. According to theoretical expectations, repeated fluctuations of population size can lead to the loss of genetic variability (Nei et al. 1975; Maruyama and Fuerst 1985). In 2 populations of *C. musculinus*, Chiappero et al. (2006) found statistically significant changes in the level

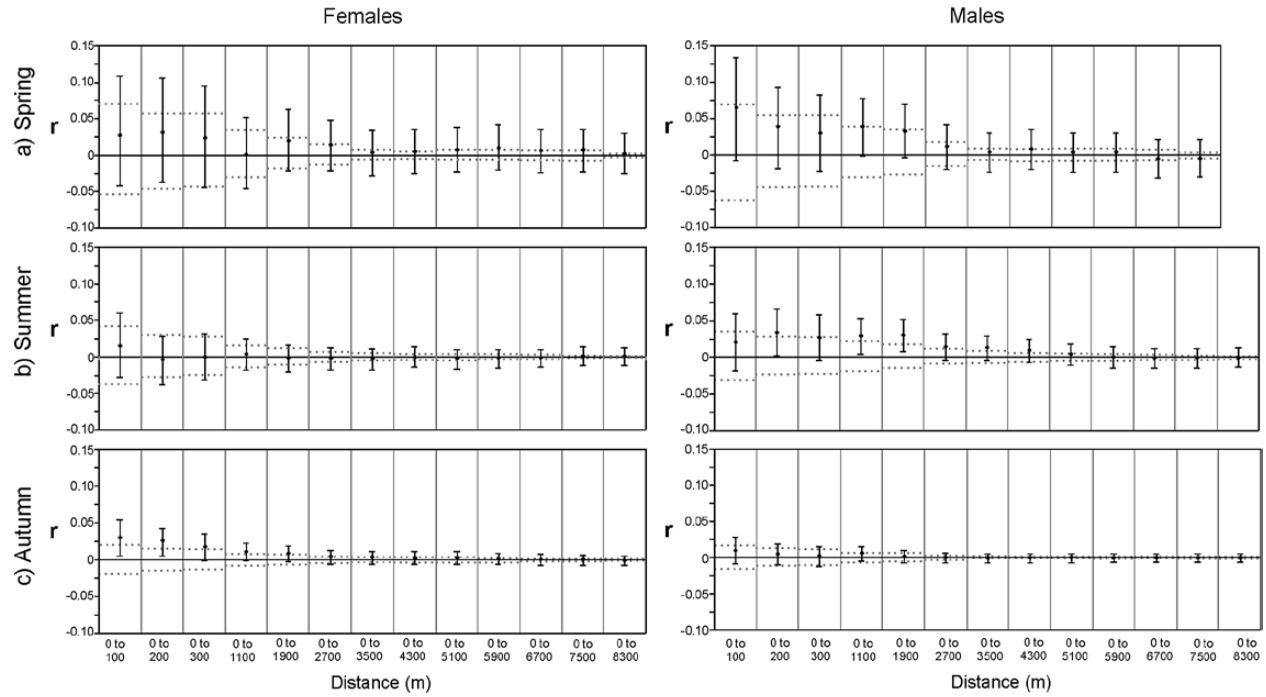


**Fig. 3.**—Spatial autocorrelation analyses of *Calomys venustus* by season and sex. a) Spring (November 2005, beginning of the breeding period); b) summer (March 2006, ending of the breeding period); autumn (May 2006, beginning of the non-breeding period); d) winter (July 2006, non-breeding period). The grey dotted line indicates the upper and lower bounds of the 95% confidence interval (*CI*) around the null hypothesis of no spatial structure ($r = 0$). The vertical bars indicate the 95% *CI* around each observed value of *r*.

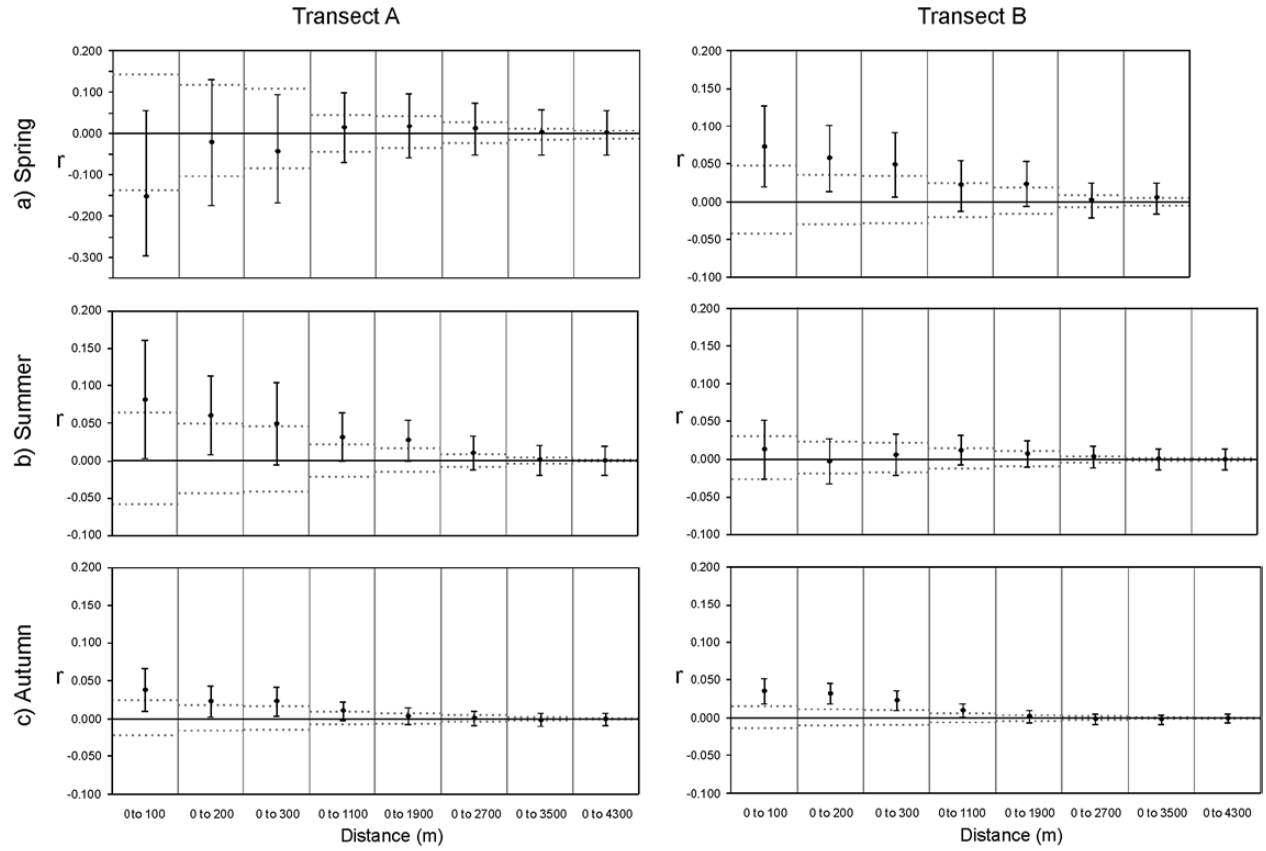


**Fig. 4.**—Spatial autocorrelation analyses of *Calomys venustus* for transects A and B by season. a) Spring (November 2005, beginning of the breeding period); b) summer (March 2006, ending of the breeding period); c) autumn (May 2006, beginning of the non-breeding period); d) winter (July 2006, non-breeding period).The grey dotted line indicates the upper and lower bounds of the 95% confidence interval (*CI*) around the null hypothesis of no spatial structure ($r = 0$). The vertical bars indicate the 95% *CI* around each observed value of *r*.

of allozymic AR, coincident with changes in $N_e$. On the contrary, in *C. venustus*, genetic variability remained high despite significant changes in population abundance: levels of Allelic Richness and $H_e$ were similar to those found in 9 microsatellite loci in the syntopic sigmodontinae rodent *C. musculinus*, a habitat generalist (Chiappero et al. 2011; Sommaro 2012) and in other rodent species (Queney et al. 2000; Aars et al. 2006; Schweizer et al. 2007), suggesting that the addition and loss of individuals across the annual cycle does not skew the genetic composition of the population, at least as reflected by these neutral loci. Similar results were found in several cyclic rodent populations like the fossorial water vole, *Arvicola terrestris* (Berthier et al. 2005, 2006), the root vole *Microtus oeconomus* (Pilot et al. 2010), the wood lemming *Myopus schisticolor* (Vuorinen and Eskelinen 2005), the red- and grey-sided voles *Myodes rutilus* and *M. rufocanus* (Ehrich et al. 2009), the greater long-tailed hamster *Tscherskia triton* (Dong et al. 2010), and several species of arctic lemmings (Ehrich and Jorde 2005).These species show multiannual population cycles, which are apparently absent in *C. venustus* although it shows irregular fluctuations, with years of higher overall abundance than others (Andreo et al. 2009). In *C. venustus,* cycles are annual, which means that the phase of low population abundance is very short, lasting only through winter and spring of each year (overwintering and 1st cohorts), followed by a fast recovery of population numbers in summer and autumn (2nd and 3rd cohorts); these seasonal phases do not lead to significant loss of genetic variability in this species.

The above cited studies in cyclic rodent species found a common pattern: no matter the amplitude of the low-density phase, the existence of dispersal resulting in genetic exchange among more or less distant areas is usually sufficient to maintain genetic variability over large areas. In particular, Aars et al. (2006) found that genetic variability in *A. terrestris* was equally high in low-density and patchy populations as in high-density, continuous populations. They observed that high levels of variability could be retained in fragmented populations when the variance in reproductive success among females was low and dispersal was frequent over long distances. *C. venustus* presents a promiscuous-polygynous mating system; males share their home ranges with both sexes, while females share theirs with several males, but not with other females. Thus, *C. venustus* females defend exclusive spaces that do not overlap with those of other females during the breeding period, regardless of population abundance. However, at high population abundances, the size of the home ranges decreases, allowing the establishment of more females per area (Priotto et al. 2002), which would contribute to lower the variance in reproductive success among females.

We found a small but significant deficiency of heterozygotes over the entire area in all seasons, indicative of weak spatial substructure. In spring, summer, and autumn (reproductive season), this was determined in part by a small but significant genetic differentiation among individuals occupying different borders (A and B compared to C and D; Table 3). Individuals living in borders separated by a secondary road showed no genetic differentiation, suggesting that gene flow across the dirt road is not restricted (Table 3).

Genetic autocorrelation was absent in winter but present in the other seasons (Fig. 2); genetic structure may be disrupted during winter, possibly because surviving animals are a random sample of the population of the previous breeding season. The positive autocorrelation at short distances in spring (Fig. 2a) suggests that when a new breeding season begins, the offspring of overwintering animals would slowly start to spread the genetic autocorrelation, as they progressively establish themselves in empty spaces in the border habitat. This would proceed faster in the narrow border, due to the limited space available (Fig. 4a). In summer, the wide border developed positive autocorrelation until 200 m, while the narrow border showed a random pattern (Fig. 4b). The total population shows a strong autocorrelation pattern until 1,900 m (Fig. 2b) and the pattern of genetic differentiation between individuals are best explained by a model in which borders pose no resistance to gene flow and crop fields offers only a weak resistance. These patterns can be explained by high levels of dispersal in this season: as density increases, empty spaces are increasingly occupied, and new individuals entering the reproductive population are forced to disperse. At the peak of population density at the beginning of the non-breeding period (autumn), the positive autocorrelation is still present until 300 m in transects A and B separately (Fig. 4c), but extending further (1,100 m) when considering the total population (Fig. 2c). In this season, the pattern of genetic differentiation between individuals can be explained by geographic separation alone (Supporting Information S4). These results suggest that, despite showing a strong preference for tall vegetation and being confined to border habitats, *C. venustus* disperses readily through non-favorable habitat such as crop fields and secondary roads. Dispersal through unfavorable habitat has been recorded for other small mammal species with particular habitat requirements. For example, Taylor et al. (2007) determined that the eucalyptus-dependent marsupial *Petauroides volans* was capable of dispersing large distances through hostile environments (pine plantations). A similar result was observed in the southern water vole *A. sapidus*, a habitat specialist of naturally fragmented habitat such as small freshwater lakes, ponds, and slow-moving streams (Centeno-Cuadros et al. 2011). Pereoglou et al. (2013) also found a generalist dispersal strategy in the postfire specialist rodent *Pseudomys gracilicaudatus*. Direct observations of movement distances in *C. venustus* indicated that, despite most individuals moved between 0 and 40 m, 6% of them moved more than 300 m; the maximum recorded distance was 1,650 for a male. Also, 8 individuals (2 males and 6 females) were observed to cross the road throughout the study (Gomez et al. 2011). Direct and indirect estimations of dispersal for *C. venustus* indicate that gene flow at the geographical scale considered in this study (approximately 25 km$^2$), combined with mating system and space use in the territorial sex (females), would prevent significant loss of variability despite large fluctuations in population size.

Gomez et al. (2011) observed that movement distances in *C. venustus* were affected by abundance and sex: males moved longer distances than females and both sexes moved less at the highest abundance. However, spatial genetic autocorrelation analyses showed that during the breeding period (spring and summer) females displayed a random structure. Males, on the contrary, showed a positive structure until 1,900 m. Priotto et al (2004) proposed that the dispersal behavior of juvenile females would be related to the territoriality of mothers during the breeding period and with the fast sexual maturation of juvenile females compared to males (35–45 days in females versus 60 days in males). In this promiscuous-polygynous species, owning a reproductive space would be an important limiting factor for females, leading to a high rate of dispersal of juvenile females. The seasonal pattern of spatial genetic autocorrelation obtained in this work would support this proposal. We observed that during the breeding period, at low and intermediate values of population densities, females show no structure indicating that they have dispersed readily from their natal area. The benefit of dispersing in an environment with available habitats to establish new territories would overcome the costs of dispersing (increased mortality due to predation, increased energy expenditure due to movement, aggressive encounters with other females, etc.—Bonte et al. 2012). Priotto et al. (2002) observed that spacing patterns of *C. venustus* females shift from territorial behavior during the breeding period to non-territorial with a high degree of intrasexual home range overlap in the non-breeding period, suggesting that females become tolerant of each other, especially their offspring. Therefore, at the beginning of the non-breeding period, at high population density, the positive spatial structure of females would relate to the ending of reproductive activity. Besides, *C. venustus* offspring born late in the breeding season postpones reproduction until the following year, as was observed in Arvicoline rodents (Lambin and Yoccoz 2001; Provensal and Polop 2008; Le Galliard et al. 2012). Thus, during the non-breeding period, females would have no motivation to disperse and, rather, remain philopatric.

Male genetic structure in the breeding period could be determined by several factors. First, Priotto et al. (2004) found that juvenile males disperse less than juvenile females in relation to the center of activity of their mothers and remain near their natal area until maturity. Second, spacing of adult males depends on receptive female distribution, and finally, the absence of territorial behavior of adult males would not lead juvenile males to disperse (Priotto et al. 2002, 2004). This is supported by spatial autocorrelation analyses performed considering females and juvenile males (Supporting Information S5). The presence of juvenile males determines a strong positive autocorrelation pattern in the 1st distance class in summer, which was absent in females and was very weak in males (Fig. 3b). In autumn, considering young males together with females causes autocorrelation to extend further than observed only for females (until 1,100 m).

In conclusion, we found that the rodent *C. venustus* living in border habitats of an agroecosystem in central Argentina maintains high levels of genetic variability, despite seasonal fluctuations in population size. Dispersion patterns depend mostly on geographic distance, with unfavorable habitats (crop fields and secondary roads) not posing a barrier to dispersal. This would result in gene flow across long distances that translate to a weak overall pattern of spatial genetic structure and contribute to maintenance of genetic variability. Female competition for reproductive space in borders likely contributes to high levels of juvenile female dispersal that, in turn, results in random spatial genetic structure among females during the breeding period. On the contrary, positive genetic structure among males may be related to delayed juvenile dispersal and intrasex tolerance.

Gelling et al. (2007) reported that in Great Britain's agricultural landscapes, linear habitats in the form of hedgerows between fields play an important role as permanent habitats, as dispersal corridors, and overall to maintain viable population sizes of several species of rodents. Our results contribute to further understanding of the role of linear habitats in agricultural landscapes by showing that although greatly reduced in area, they can support populations of species without loss of either variability or genetic connectivity.

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## Supporting Information

The Supporting Information documents are linked to this manuscript and are available at Journal of Mammalogy online (jmammal.oxfordjournals.org). The materials consist of data provided by the author that are published to benefit the reader. The posted materials are not copyedited. The contents of all supporting data are the sole responsibility of the authors. Questions or messages regarding errors should be addressed to the author.

Supporting Information S1.—Amplification conditions of 6 microsatellite loci for *Calomys venustus*.

Supporting Information S2.—*Calomys venustus* captured each season, discriminated by transect and sex.

Supporting Information S3.—*f* values by locus, season, and transect.

Supporting Information S4.—Results of seasonal Mantel and partial Mantel tests for isolation by resistance analyses.

Supporting Information S5.—Spatial autocorrelation between females (adults and juveniles) and juvenile males.

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