

Relatedness dynamics and sex-biased dispersal in a seasonal cycle of corn mice from intensively managed agroecosystems

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Abstract

The sex-biased dispersal and kinship dynamics are important factors shaping the spatial distribution of individuals and are key parameters affecting a variety of ecological and evolutionary processes. Here, we studied the spatial distribution of related individuals within a population of corn mice *Calomys musculinus* in a seasonal cycle to infer dispersal patterns. The sampling was carried out from spring 2005 to winter 2006 in field borders of intensively managed agroecosystems. Genotyping data from 346 individuals with 9 microsatellites showed spatial genetic structure was weak for males, but not for females. The results indicate a complex spatial kinship dynamic of related females across all seasons. Which, contrary to our expectations, dispersal distances decrease with the increase of the population abundance. Meanwhile, male dispersal distances were greater when population abundance increased and thus the availability of active females. Males disperse greater distances to mate and sire offspring with distant females as a possible inbreeding avoidance mechanism. This study shows that *C. musculinus* is capable of much greater scattering distances than previously reported and that dispersal occurs fluidly and without barriers across the agroecosystem. The indirect benefit of dispersal on individual fitness could be related to relaxing the competition in the natal area and increasing the mating rate. Our study highlights the value of combining genetic relatedness, fieldwork observations, and behavioral data to estimate dispersal at a fine geographical scale.

Key words: dispersal distances, kinship dynamics, microsatellite, small mammals, spatial autocorrelation.

Dispersal is broadly defined as the movement of individuals from natal or breeding site to another. Therefore, dispersal results in the redistribution of organisms and their genes, both within and between populations with potential consequences for gene flow across space (Ronc 2007; Matthysen 2012; Mabry et al. 2013; Spiegel et al. 2017; Saastamoinen et al. 2018). Dispersal is a fundamental process in ecology and evolution because it strongly influences the population's genetic structure, dynamics, and persistence. Additionally, it provides insights into inbreeding avoidance, kin competition, and cooperation (Lawson Handley and Perrin 2007; Meier et al. 2011; Clobert et al. 2012).

In small mammals, it is meaningful to consider the frequency and distances of dispersal relative to their home range, and its relationship with the prevailing ecological conditions (e.g., population density) (Bowman et al. 2002;

Costello 2010; Spenser 2012). Detecting genetic structure at a fine-geographic scale where individuals are highly mobile and can disperse distances well in excess of their home ranges, provides important insights into the dispersal patterns and social structure of a species (Cuttler et al. 2005; Lacey and Sherman 2008) across varying environmental conditions (i.e., Busch et al. 2009; Dubuc-Messier et al. 2012; Mabry 2014). Besides, dispersal relative to the home range may differ between sexes, with male-biased dispersal and female philopatry being the most common pattern (Greenwood 1980; Mabry et al. 2013). At a fine spatial scale, sex-specific philopatry can generate a spatial genetic structure (hereafter SGS) as a result of the nonrandom distribution of genotypes (Peakall et al. 2003; Blackmore et al. 2011; Binns et al. 2020). Besides, mating behavior may modify the patterns of SGS (Mabry 2014; Garcia-Navas et al. 2016). For example, the

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“kin cooperation” hypothesis (Silk 2007; Lacey and Sherman 2008) predicts that greater SGS in females may imply the existence of matrilineal clusters, which provides fitness benefits in the form of defense against unfamiliar conspecifics (e.g., infanticidal females; Wolff and McDonald 2004).

The agroecosystems of central Argentina present a remarkable spatiotemporal variability due to yearly land-use activities (i.e., harvest and plow activities) (Fraschina et al. 2012; Serafini et al. 2019). Therefore, they offer a particularly interesting scenario to explore the spatial and temporal distributions of wild animal genotypes in human-modified landscapes (Chiappero et al. 2016; Vera et al. 2019). Argentinean agroecosystems consist of monocultures of a few crops (corn, soybean, sunflower, and wheat) surrounded by a network of roadsides, fence lines, railways, and other border habitats that keep remnants of native flora and many introduced weeds. These linear areas serve as a refuge for small mammals and also as corridors throughout croplands (Gomez et al. 2015; Serafini et al. 2019). One of the most abundant rodent species in these habitats is the corn mouse, *Calomys musculinus* (Cricetidae: Sigmodontinae), a short-lived species, relatively easy to trap and mark, that reproduces quickly. They have a promiscuous social and genetic mating system with high rates of multiple paternity during the breeding period, which lasts approximately 8 months (Mills and Childs 1998; Steinmann et al. 2009; Sommaro et al. 2015). Population abundance varies seasonally associated with natural variations in climatic variables and land-use management that affect the availability of resources (Andreo et al. 2009). As population abundance increases (i.e., late summer and early autumn), males' home range size and overlap degree with those of both sexes decrease, while females keep their home ranges size and exclusivity (Steinmann et al. 2005, 2006; Sommaro et al. 2009, 2010a). In the nonbreeding period, male and female home-range sizes remained similar (Steinmann et al. 2005, 2009).

Movement distances inferred by capture–recapture data in linear habitats vary seasonally, being smallest in autumn and highest in spring, and also larger in males than in females (Sommaro et al. 2010b). These previous studies measured the movement of individuals but not the effectiveness of dispersal (i.e., successful reproduction after immigration), since the movement of individuals may be different from effective dispersal resulting in gene flow within and among demes (Prugnolle and de Meeus 2002; Fontanillas et al. 2004). Here, we studied the spatial distribution of individuals with different degrees of genetic relatedness within a wild population of *C. musculinus* in a seasonal cycle. We aimed to assess the spatiotemporal variability of the relatedness structure (Croft et al. 2021) to gain insights into the flexibility of the social structure and factors influencing the dispersal patterns of corn mice, a species abundant in intensively managed agroecosystems.

According to the female-biased philopatry hypothesis, we expect to find shorter dispersal distances and greater SGS in females than in males across seasons. Moreover, as *C. musculinus* individuals tend to modify their spacing and movement distance behavior with increasing population abundance, we expect SGS and sex-specific dispersal distances to change at different moments of the annual breeding cycle. Indeed, *C. musculinus* females compete for the availability of breeding spaces and males compete for access to estrous females (Steinmann et al. 2005, 2009; Steinmann and Priotto 2011). In summer, we expect females to disperse over greater distances

and show a decrease in SGS at high population abundance due to low breeding space availability. In males, however, we expect them to show the inverse pattern, high SGS, and short dispersal distances, due to the greater availability of females at increasing population abundances.

Materials and Methods

Study species

Calomys musculinus is a small-sized rodent (22 g) and widely distributed in southern South America, particularly in the Pampean ecoregion (de Villafañe 1981; Busch et al. 2000, 2005; Porcasi et al. 2005). It is considered an extreme generalist in terms of its dietary and habitat preferences. In addition, it is a good settler of disturbed habitats and shows a wider habitat and trophic niche than other coexisting rodent species (Martínez et al. 2014; Gomez et al. 2015; Serafini et al. 2019). Populations of the corn mice are characterized by a seasonal variation in abundance: with lower values, even close to zero, during the winter and spring (16 individuals/ha) and peaks during late summer and autumn (260 individuals/ha). Cold periods are energetically demanding, affecting the survival of this species (Busch and Kravetz 1992). Moreover, a 1:1 sex ratio is common (Mills et al. 1991; Mills and Childs 1998; Sommaro et al. 2010b). In semi-natural enclosures, laboratory-raised mice were captured for up to 6.7 months (200 days of age), whereas overwintering adults from the wild survived approximately 5.3 months (Sommaro et al. unpublished). The breeding period extends from September to April and the sexual maturation of juveniles is independent of adult presence (between 32 and 40 days of age). The gestation period is short (21 days) and each female, on average, gives birth to 6 pups per litter and several litters during its lifetime (at least 5 mating events) since have a high frequency of postpartum estrus (de Villafañe 1981; Busch et al. 2000; Sommaro et al. 2009). During the breeding period, females also keep exclusive home ranges regardless of population abundance and defend themselves through highly aggressive behavior toward other females to avoid infanticide (Sommaro et al. 2009; Coda et al. 2011). Males' home ranges are fully shared with both sexes and are more than twice as large as those of females (average values: 535 m² for males and 240 m² for females) (Steinmann et al. 2005, 2006).

Study site and sampling

This study was carried out from November 2005 to July 2006 in linear habitats of agricultural ecosystems in Río Cuarto Department (Córdoba Province, Argentina). Despite the influence of crop fields, borders have a homogeneous plant cover of about 85% throughout the year and high availability of seeds in the soil (Priotto et al. 2002). Four sampling transects located in field borders were used as study sites, 1 placed on a wide border (range of width: 10–30 m; transect A) and 3 placed on narrow borders (2 m; transects B, C, and D). Sampling transects were set up on opposite sides of 7-m-wide secondary roads (A opposite B; C opposite D). Each transect was composed of 300-m trap lines with 30 Sherman-type traps spaced at 10-m intervals. Trap lines were separated by 500 m. Transects A and B each had 5 trap lines each (A1, A2, A3, A4, A5, B1, B2, B3, B4, and B5) and transects C and D each had 3 trap lines each (C1, C2, C3, D1, D2, and D3). The total transect length was 3,800 m for transects A and B, 1,900 m for transects C and D (Figure 1). Each trap was checked once

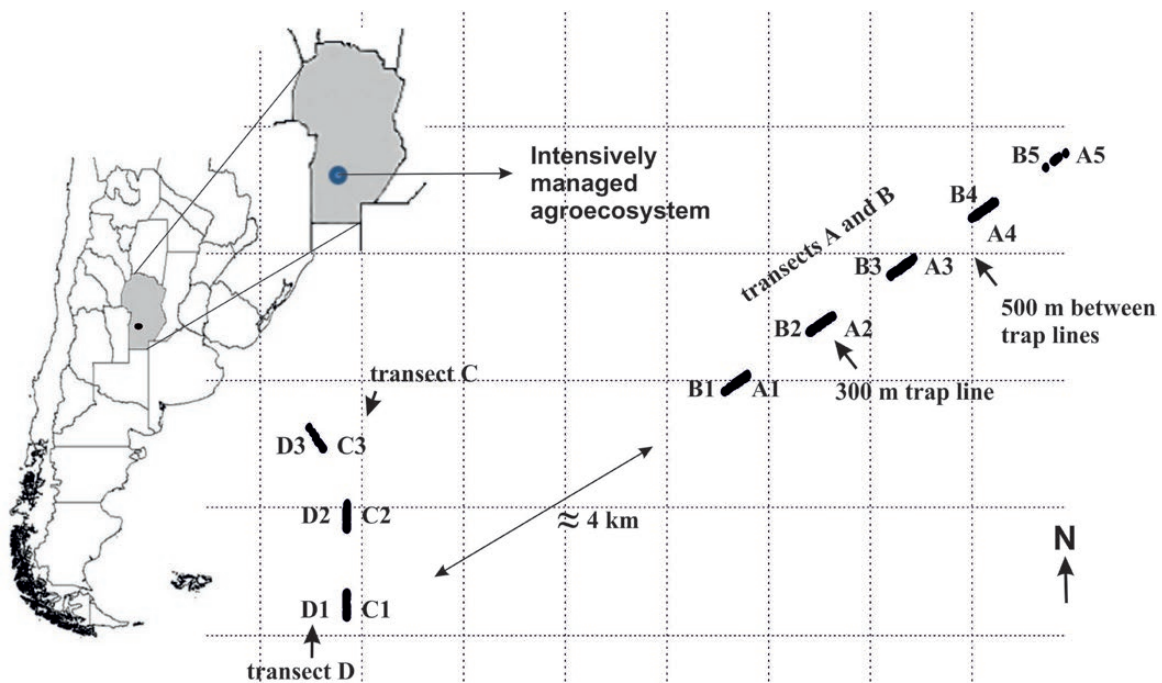


Figure 1. Map of the geographical distribution of transects in the study area. The trap lines were set up on opposite sides of secondary roads in linear habitats of an agricultural ecosystem in Río Cuarto Department (Córdoba Province, Argentina).

a day in the morning. Capture, mark, and recapture trapping sessions were conducted for 5 consecutive days in November (spring), March (summer), May (autumn), and July (winter). Each capture site was georeferenced with a GARMIN eTrex Legend Cx GPS. Trapped animals were weighed and marked with self-piercing ear tags with numerical codes (National Band and Tag Company, Newport, Kentucky) or small ear cuttings with scissors. We determined the sex (based on anogenital distance), body mass (by weighing with a Pesola spring scale), body length (using a tape measure), and approximate age according to weight (juveniles ≤ 9 g and adults > 10 g for spring and summer; adults > 9 g for autumn; in winter, all individuals were considered adults) (Steinmann et al. 2005; Sommaro et al. 2009). In males, the reproductive condition was determined by whether the testes were abdominal or scrotal, and in females, by whether the nipples were enlarged (probably pregnant or lactating) and the vulva was perforated or imperforated. Before releasing each captured individual, a small piece of the tail tip was collected and preserved in ethanol for DNA analyses. Research on live animals was performed in a humane manner and followed guidelines for the care and use of animals approved by the American Society of Mammalogists (Sikes et al. 2019) and current Argentinian Laws (National Law 14346).

Microsatellite genotyping

DNA was extracted using DirectPCR (Tail) (Viagen-Biotech Inc., Los Angeles, CA) following the manufacturer's instructions and resuspended in distilled water. Samples were genotyped using 9 specific microsatellite loci described by Chiappero et al. (2005) and Chiappero et al. (2011) following the authors' protocols. We observed that the molecular size of alleles in locus Cmu11 differs clearly between *C. musculus* and the syntopic species *C. venustus*, whose juveniles can be misidentified as *C. musculus*. In order to avoid including individuals from other species in our database, all samples

were first amplified for locus Cmu11 (Chiappero et al. 2005). Locus Cmu13 displays low polymorphism, with an allele in high frequency and several with low frequency. Both loci (Cmu11 and Cmu13) were separated by electrophoresis on 8% native polyacrylamide vertical gels using the Tris-Glycine buffer system (White et al. 2000) and stained with silver nitrate (Neilan et al. 1994). Allele sizes were inferred by comparison to molecular size standard (10 bp DNA Ladder; Invitrogen). Microsatellite loci Cmu1, Cmu2, Cmu3, Cmu4, Cmu14, Cmu15, and Cmu17 were amplified with fluorescently labeled forward primers (6FAM, VIC, NET, and PET dyes), and fragment length was analyzed with an ABI 3730XLs automatic sequencer at Macrogen Inc. (Seoul, Republic of Korea), and allele sizes scored using PeakScanner (Applied Biosystems Inc, 12/2006) and MsatAllele package v1.05 in R (Alberto 2009). MsatAllele is used to visualize and bin the raw microsatellite allele size distributions. In this program, the bin limits are not fixed and are automatically defined based on the raw data of microsatellite lengths stored in an R database.

The GenAlEx v.6.503 program (Smouse and Peakall 2012; Smouse et al. 2017) was used to test for deviations from Hardy-Weinberg Equilibrium (HWE) by locus for each season, using the exact test. We adjusted *P*-values of HWE tests using Bonferroni correction. To avoid using individuals from more than 1 generation as a possible factor that could cause departures from HWE, we performed an additional test of HWE using overwinter spring data. The adults from this season fall in 1 of 2 categories: overwintering individuals (> 15 g females and > 25 g males) and individuals born very early at the beginning of the reproductive period (35–40 days) before the start of the spring trapping session. Additionally, our dataset was checked for unexpected mutation steps, unusually sized alleles, and null alleles using the Micro-checker software (Van Oosterhout et al. 2004). The mean number of effective alleles (N_e); observed (H_o) and expected heterozygosities (H_e), and the inbreeding coefficient (F_{IS}) were also calculated per season using Genalex.

Spatial genetic structure analyses

We conducted spatial genetic autocorrelation analyses in GenAlEx 6.503 (Smouse and Peakall 2012; Smouse et al. 2017). It estimates the maximum extent and magnitude of the detectable nonrandom genetic structure from pairwise squared genetic and geographical distance matrices. GenAlEx calculates the autocorrelation coefficient r_c as a measure of the genetic similarity between pairs of individuals whose geographic separation falls within the specified distance class. It uses as input a pairwise individual-by-individual genotypic distance matrix and a geographic distance matrix created from the GPS coordinates for each captured individual. The recapture rate was very low (1.3% within the trapping sessions and no interseason recapture). For individuals that were captured more than once, the first capture location was used. We evaluated seasonal SGS of adult males and females with the Multi DClass option (cumulative distance classes' analysis). Each sex-season combination was considered a population. In the winter season, we used all captured females and males due to the low weight of individuals which prevented us from establishing age classes. The low number of juveniles in the other seasons did not allow us to estimate SGS for this age class. Analyses were conducted considering distance classes between 0 and 7,500–7,900 m (approximately) with 100-m bins. Statistical significance was assessed with 9,999 bootstrap permutations for both within and among distance class estimations. According to Peakall et al. (2003), statistically significant positive genetic structure occurs when r_c estimation for a given distance class exceeds the 95% confidence interval about the null hypothesis of 0 and when the 95% error about r_c does not intercept the x -axis at $r_c = 0$ (Peakall et al. 2003). Each r_c value has a 1-tailed test associated; if the probability is less than 0.05, the alternative hypothesis of significant SGS is accepted. To obtain a view on a very fine scale in females, additional tests were conducted at a 200-m distance with 10-m bins (using Multi DClass option).

Relatedness and parentage estimation

The performance of different relatedness estimators has been shown to depend strongly on the data set (Harrison et al. 2013; Robinson et al. 2013; Taylor 2015); therefore, we estimated the best pairwise relatedness index for our data with the package *related* (Pew et al. 2015) as detailed in Escoda et al. (2017). Allele frequencies of the total dataset were used to simulate 2,000 individual genotypes representing 250 dyads for each of the following relationships: parent-offspring, full-siblings, half-siblings, and unrelated individuals. Relatedness for each simulated dyads was estimated using 5-moment estimators of relatedness (lynchli [Li et al. 1993], lynchrd [Lynch and Ritland 1999], quellergt [Queller and Goodnight 1989], ritland [Ritland 1996], and wang [Wang 2002]) and 2 maximum-likelihood estimators (dyadml [Milligan 2003] and trioml [Wang 2007]). The performance of all estimators was evaluated by calculating the correlation (Pearson's R) between the estimates of relatedness from simulated dyads and the expected values for each category (i.e., $r = 0.5$ for parent-offspring and full-siblings; $r = 0.25$ for half-siblings and $r = 0$ for unrelated individuals). The best estimator was selected for the highest correlation between the simulated and expected values. Using the best estimator, dyadml (Table S1), pairwise relatedness among the 346 corn mice was then calculated, using all

specimens for allele frequency estimation. Confidence intervals of 95% for relatedness values were calculated using 100 bootstrap replicates over loci. Contemporary dispersal (1 and 2 generations ago) was estimated only for second-degree relationships and higher (half-siblings, full-siblings, and parent-offsprings) since *C. musculus* present cases of multiple male mating, indicating that offsprings from the same litter could be sired by different males (Sommaro et al. 2015), the omission of half-siblings could be misleading in order to estimate contemporary dispersal patterns. The threshold value was estimated according to the lower 95% confidence interval for half-siblings for the dyadml estimator (mean relatedness = 0.2959; $SD = 0.1290$; 95% $CI = 0.2797$ – 0.3119) obtained in the simulation analysis. All the relatedness dyads equal to and above 0.2797, except for those involving individuals from different seasons, were considered for further analysis.

The parentage of each individual was estimated in each season using different datasets. On one hand, each season's cohort was used as candidate parents for all following season datasets, and on the other hand, in the same season, we used individuals classified as adults as candidate parents. A second run also included individuals that might have reached sexual maturity but are too light to be considered adults as candidate parents (individuals with 1 or 2 g below the threshold value to be considered adults). Paternity, maternity, and full- and half-siblings were assigned with the maximum-likelihood approach of the program Colony2 using the pairwise method (Jones and Wang 2010). For each run of Colony2, we set the probability that potential mothers or fathers were included in the dataset to 0.90 and used a medium run length for the full likelihood with high precision. We selected the mating system option as "polygamy" and ran these parameters 5 times to find the best configuration for each dataset. We finally selected the relationships with the highest likelihood ($P \geq 0.80$).

Dispersal distances

We calculated the Euclidean distances from geographic coordinates between dyads with the relatedness values of second degree and higher (half-siblings, full-siblings, and parent-offsprings). We then performed a multiple regression analysis with distance as a response variable and sex (male and female), season (spring, summer, autumn, and winter), and relatedness as explanatory variables. We also explored all second-order and third-order interactions between these variables. We used a backward selection procedure in the package Mass v.7.3-55 (FrF and Ripley 2011) for R 4.1.0 (R Development Core Team 2011), sequentially removing the least significant term from the model based on its P -value ($\alpha = 0.05$). As dispersal distances did not follow a normal distribution, they were rank transformed (Dubuc-Messier et al. 2012). The importance of effects was estimated by looking at the Akaike information criterion (AIC) and using a value of delta AIC < 2 to identify the best model (Burnham et al. 2011).

The estimated pedigrees were used to assess if individuals of different sex exposed to the same environment (i.e., siblings sharing a territory) opt for a similar dispersal strategy (Garcia-Navas et al. 2016). We computed for each female the dispersal distances between mother-daughter and mother-son, as well as between full-siblings: sisters and sister-brother dyads. Males were not considered as they do not keep exclusive home ranges.

Results

A total of 348 presumed *C. musculus* were trapped during a seasonal cycle in an intensively managed agroecosystem. After genotyping, 2 individuals were identified as *C. venustus* and were not considered for the statistical analyses. The number of sampled individuals varied among seasons; in spring, autumn, and winter, we captured more males than females, while in summer, the number of captured males and females was similar (Table 1). Genotype data from 346 individuals revealed high levels of genetic diversity at the 9 microsatellite loci analyzed. The number of alleles per locus ranged from 12 for Cmu4 to 46 for Cmu3, with an average value of 24 alleles. The number of effective alleles was similar in the four seasons (Table S2). High genetic variation was detected in terms of both expected heterozygosity (mean H_E across seasons: 0.856 ± 0.018) and observed heterozygosity (mean H_O across seasons: 0.688 ± 0.025), with the highest values in summer (0.722 and 0.876, respectively). The highest F_{IS} values were observed in winter (0.226) and autumn (0.216), while in summer, values were the lowest ($F_{IS} = 0.181$). The combined probability of exclusion was 0.9973 (Table S2). Micro-checker analysis revealed no large allele dropouts and detected scoring errors due to stuttering in three loci. All loci showed low frequency for null alleles between 4% and 19% (Table S2c). The frequency of null alleles was not greater than reported in other studies to estimate relatedness (Sommaro et al. 2015; Chen et al. 2022; Martella et al. 2022). In addition, Dakin and Avise (2004) showed that the presence of null alleles in frequencies lower than 20% does not cause any significant bias or error in parentage analyses. Deviations from HWE were observed across seasons (Table S2). However, the overwinter spring dataset showed deviations from HWE in 1 (Cmu11) microsatellite locus (Table S2). Therefore, this suggests that overlapping generations are the most ecological contributor to the HW disequilibrium. Even though those loci presented evidence for the occurrence of null alleles, we included them in further analyses due to their high polymorphism following Wagner et al. (2006).

Fine-scale spatial genetic structure

The SGS differs between sexes, to a greater extent in females than in males. In spring, SGS was present up to 900 m in females (except for the first 100-m distance class) and showed large confidence intervals around the estimate of rc ($rc = 0.023$; $P = 0.139$; $Lr = -0.022$; Figure 2A). In summer (Figure 2B), female's SGS was positive and significant from 100 to 3,100 m. In autumn, SGS was positive and significant from 200 m up to 1,200 m ($P < 0.05$) (Figure 2C). In winter (Figure 2D), females showed positive SGS but nonsignificant rc up to 800 m (complete results in Table S3). Additional analyses at a very

fine scale (200 m total distance with 10-m bins) revealed that females showed positive and significant SGS at 150 m in spring, 60 m in summer, and 20 m in autumn (Figure S1). Males did not show significant SGS in spring and autumn (Figure 3A,C). In summer, males presented SGS with positive rc and significant 1-tailed P -values from 0 to 100 m and from 300 to 1,100 m. But, the lower 95% confidence interval was negative in all distance classes (Figure 3B). In winter, males present positive and significant SGS up to 900 m (Figure 3D). Furthermore, the correlation coefficient rc was greater for females than for males, a pattern that was especially evident in spring (Table S3).

Relatedness and parentage

The best relatedness estimator for our dataset was dyadml (Milligan 2003), a maximum-likelihood estimator which yielded a total of 59,685 dyads for all kinship relationships: parent-offspring, full-siblings, half-siblings, distant kinship relationships (grandparent-grandchild, first cousins), and unrelated individuals. In maximum-likelihood methods, estimates of kinship and consanguinity are limited to values greater than 0 due to their probabilistic nature; thus we excluded relatedness estimates when the lower 95% confidence limit of the bootstrap replicas was equal to or below 0, despite the estimate of relatedness being higher than 0. Thus, our dataset with close and distant kinship relationships (with lower 95% CI > 0) had 1,525 dyads; the minimum pairwise relatedness was 0.1341, the maximum was 1.419, and the average was 0.4207.

To estimate dispersal distance between highly related individuals, we only keep dyads with a relatedness value equal to or higher than 0.2797 (close kinship relationships: parent-offspring, full-siblings, and half-siblings) and dismissed those below this value (distant kinship relationships). This dataset of close kinship relationships was composed of 1,394 dyads belonging to 342 individuals out of a total of 346. That means that most of the individuals captured were assigned to a close kinship relationship at least once. We found, in total, 307 dyads of highly related individuals occurring in the same season.

Parentage analysis identified 114 different dyads: 34.21% (39) parent-offspring, 6.14% (7) full-siblings, and 59.64% (68) half-siblings (Table S4). Twenty-seven of 39 parent-offspring assignments (69%) were from interseason dyads, reflecting the permanence of the individuals at the sampling site. Only 4 father-son/daughter and 8 mother-son/daughter relationships corresponded to intraseason.

Patterns of dispersal distances

The maximal distances for dyads were observed in summer, in females was 8,225.4 m (relatedness, $r = 0.46$) whereas for

Table 1. Distribution of 346 individuals of *Calomys musculus* caught in border habitats of an agroecosystem and genotyped for 9 microsatellite loci

Description	Spring	Summer	Autumn	Winter	Total
Total sample size	82	134*	77	53	346
Adult males	52	63	32	38	
Adult females	27	64	27	15	
Juvenile males	1	3	9		
Juvenile female	2	3	9		

Males and females are seasonally discriminated into adults and juveniles. (*) One adult with undetermined sex.

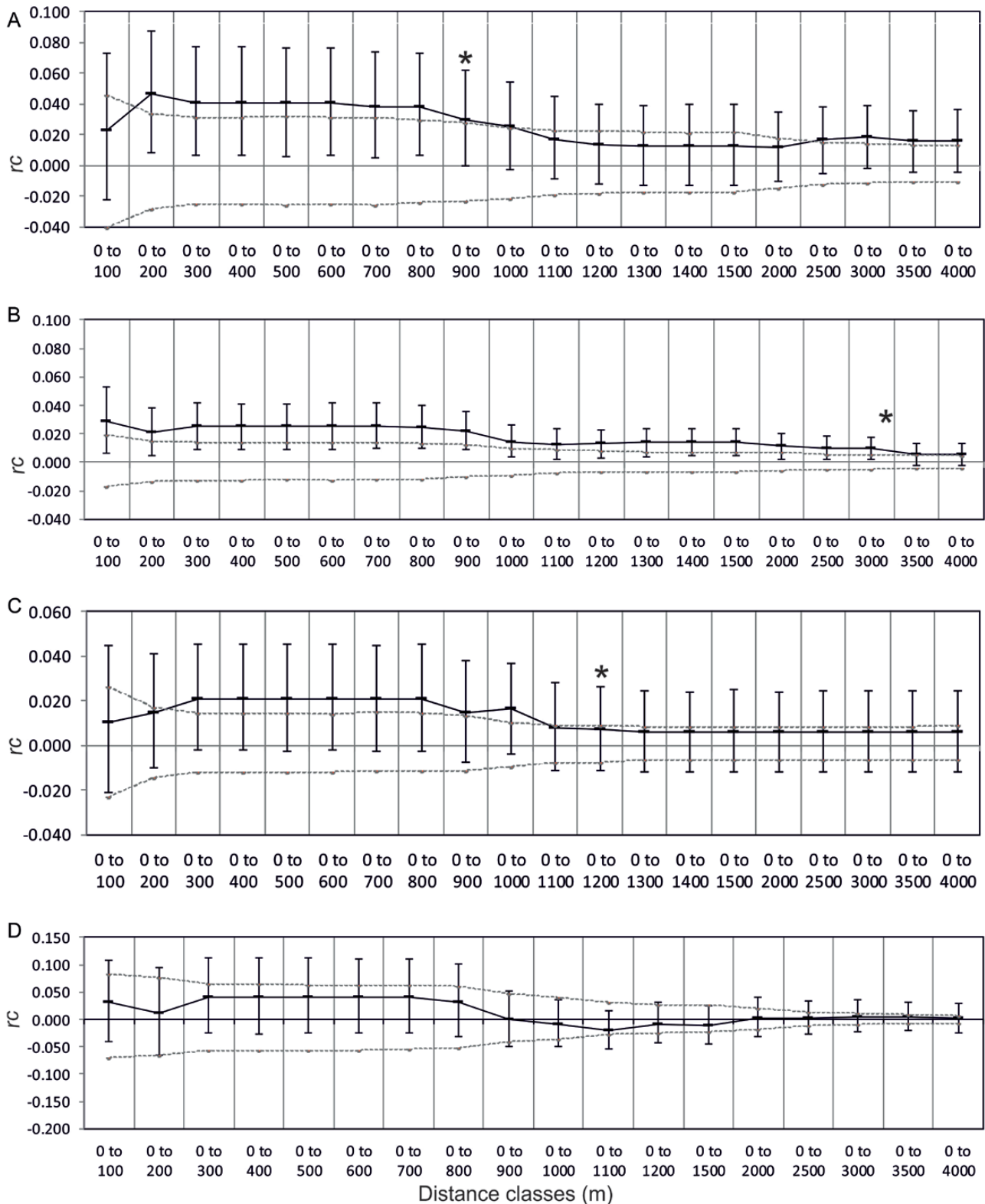


Figure 2. Seasonal spatial genetic structure at multiple distance class sizes detected in adult females of *Calomys musculus* in border habitats of an agroecosystem (Cordoba, Argentina) in (A) spring; (B) summer; (C) autumn, and (D) winter. The horizontal bars connected by the solid line show the (rc) spatial autocorrelation coefficient for each distance class, note that from 1,500 m the distance classes are larger. The asterisk indicates the extent of genetic structure with significantly positive " rc " values with the 1-tailed test ($P < 0.05$). The dotted lines indicate the upper and lower bounds for the 95% confidence interval about the null hypothesis of no spatial structure ($rc = 0$) obtained by 1,000 random permutations of genotypes among distance classes. The vertical bars indicate the 95% confidence interval around " rc " obtained by 1,000 bootstrap resamplings within each distance class. Complete values in Supplementary Material.

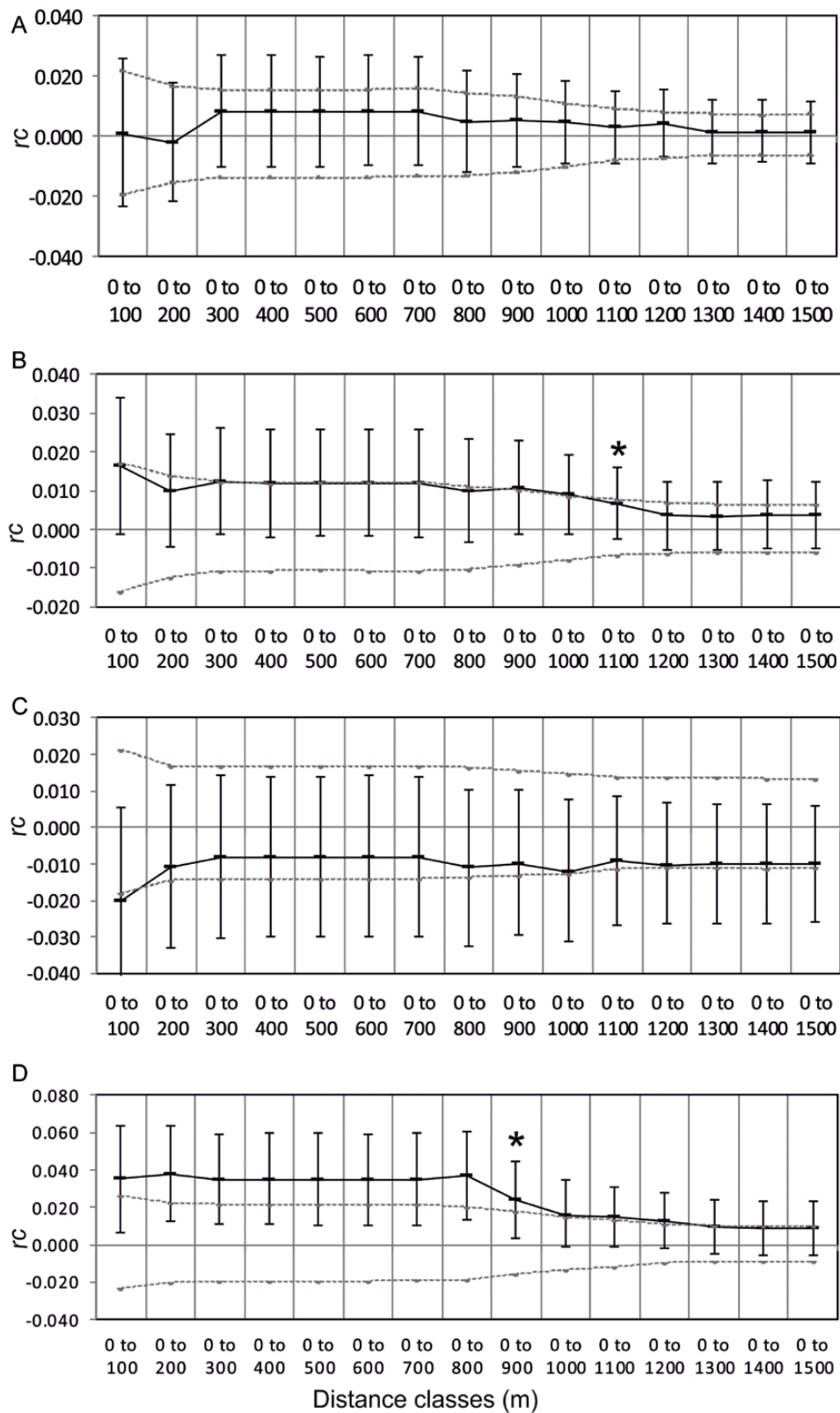


Figure 3. Seasonal spatial genetic structure at multiple distance class sizes detected in adult males to *Calomys musculus* in border habitats of an agroecosystem (Cordoba, Argentina) in (A) spring; (B) summer; (C) autumn; and (D) winter. The horizontal bars connected by the solid line show the (rc) spatial autocorrelation coefficient for each distance class up to 1,500 m. The asterisk indicates the extent of genetic structure with significantly positive " rc " values with the 1-tailed test ($P < 0.05$). The dotted lines indicate the upper and lower bounds for the 95% confidence interval about the null hypothesis of no spatial structure ($rc = 0$) obtained by 1,000 random permutations of genotypes among distance classes. The vertical bars indicate the 95% confidence interval around " rc " obtained by 1,000 bootstrap resamplings within each distance class. Complete values in Supplementary Material.

a male dyad was 9,170.36 m ($r = 0.347$). The mean distance for female dyads also was greater in summer (2,684.584 m), whereas for male dyads, the mean distance was greater in autumn (4,128.746 m) and shorter in winter (2,487.36 m) (Table 2 and Figure 4). Nevertheless, due to the wide range of dispersal distances observed in all categories, we also calculated the median of the dispersal distance. Notably, we could observe that the typical dispersal distance traveled by the female dyads decreased toward the end of the breeding season, whereas for males, the typical dispersal distance travelled increased (Table 2).

The optimal multiple regression model (Table S5) explained 9.75% of the variance in the data. There is an inverse relationship between dispersal distances and their relatedness (Table 3). Highly related males tend to reach longer dispersal distances than females (Table 3), which tend to be more philopatric. For both sexes, distances increased in spring and summer in comparison to autumn (Table 3). The frequency of dispersal distances in males is more equally spread than in females during spring, summer, and autumn and drops in winter for both sexes (Table 3 and Figure 4).

Although the dispersal distances estimated showed a very wide variation, it was possible to estimate the spatial distribution of the individuals according to sex and kinship. Sons scattered further from their mother's territory than did daughters (98.07 vs. 27.95 m) (Table 4). Spatially, female offspring (full sisters) settled close to each other in comparison to half-sister females (from the same litter or not) which settled further apart between them (207.77 vs. 1334.33 m). Female full-siblings were more widely spaced than their male full-siblings. The median distance between full-sibling female dyads was 207.77 m and full-sibling female–male was 22.69 m. We did not compare these values statistically since the small sample size and the fact that we did not register full-sibling male dyads.

Discussion

Dispersal is a complex trait with different aspects including the rate, distance distribution, and the timing of dispersal relative to mating (Li and Kokko 2019). As suggested for most mammals (Greenwood 1980; Mabry et al. 2013), *C. musculus* males in our study population dispersed more frequently and further away than females. Contrary to our expectations,

Table 2. Seasonal description of distance between dyads (m) of closely related (parent–offspring, full-siblings and half-siblings) corn mice in agroecosystems from Río Cuarto (Córdoba, Argentina)

Season	Females' dispersal distance (m)			Males' dispersal distance (m)		
	Mean	Median	N	Mean	Median	N
Spring	2,541.35	2,067.45	27	3,209.95	2,375.43	46
Summer	2,684.58	1,168.62	68	3,816.89	2,761.12	64
Autumn	1,637.92	209.78	39	4,128.75	5,465.86	38
Winter	-	-	-	2,487.36	1,129.69	24

Sex, mean, median and sampling size (N) are detailed.

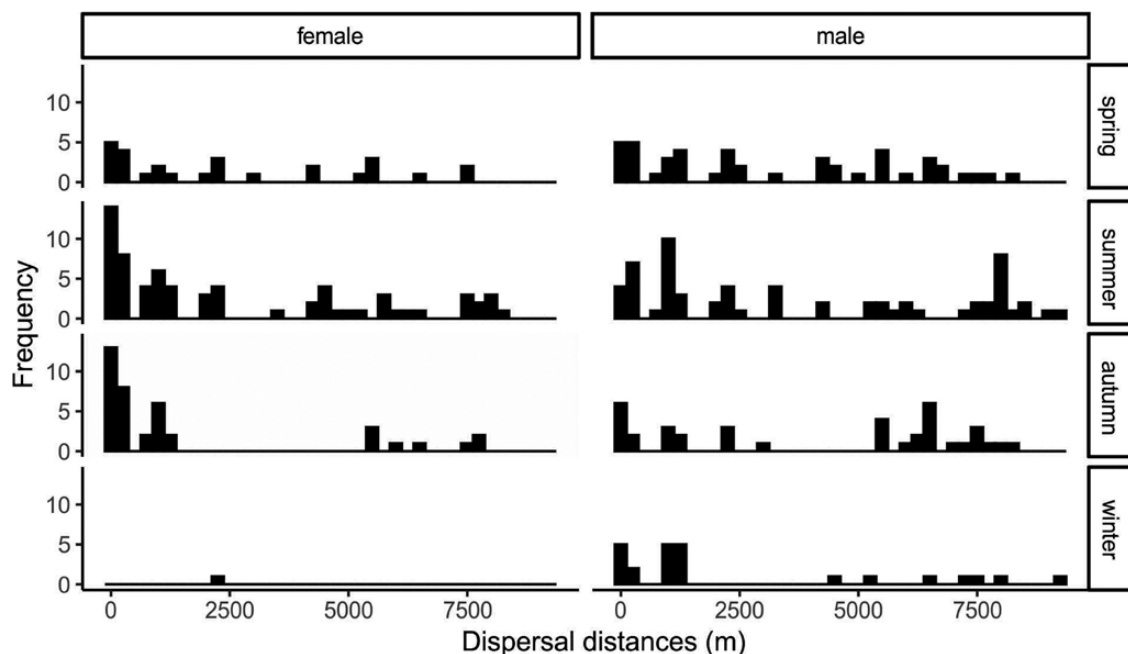


Figure 4. Geographic distances between highly related individuals ($r \geq 0.2959$) of *Calomys musculus* in agroecosystems of Río Cuarto (Argentina), histograms of dispersal distances across the seasons (spring, summer, autumn, and winter) for female and male dyads, respectively.

Table 3. Model (Sex × Season + relatedness) explaining dispersal distances based on genetic relatedness of second-degree (half-sibs) and higher (full-sibs and parent–offsprings) relationships in a population of corn mice from agroecosystems near Río Cuarto (Córdoba, Argentina)

	Coefficient ± SE	t-Value	P
Intercept	150.38 ± 22.03	6.826	<0.0001
Sex: male ^a	77.85 ± 19.38	4.017	<0.0001
Season: spring ^b	45.68 ± 21.16	2.159	0.032
Season: summer ^b	40.77 ± 16.99	2.399	0.017
Season: winter ^b	47.16 ± 85.59	0.551	0.582
Relatedness	-106.74 ± 36.18	-2.951	0.003
Sex × Season: male-spring ^c	-59.15 ± 28.06	-2.108	0.036
Sex × Season: male-summer ^c	-42.72 ± 24.22	-1.764	0.079
Sex × Season: male-winter ^c	-91.42 ± 88.39	-1.034	0.302

Significant effects ($P < 0.05$) are in bold. The adjusted R-square is 9.75%. $N = 307$ individual pairs.

^aFemale is the reference.

^bAutumn is the reference.

^cMale-autumn is the reference.

Table 4. Dispersal distance (D) in meters between dyads (N) from sibling categories (FS: full-siblings; HS: half-sibling) and mother–offspring relationships in agroecosystems corn mouse population from Río Cuarto (Córdoba, Argentina)

Categories	Range of D	Median D	Mean D	N
Mother–daughter	11.04–7,716.54	27.95	2,210.79	6
Mother–son	0–8,387	98.07	2,228.29	8
FS female–female	80.55–1,050.36	207.77	446.22	3
FS female–male	7.44–92.05	22.69	36.22	4
HS female–female	46.19–7,592.51	1,334.33	2,586.21	16

Data obtained from pedigree results.

in summer and autumn, dispersal distances registered by most of the male dyads were greater when population abundance increased and thus the availability of active females. Astonishingly, females presented higher dispersal distances according to their spacing behavior. Besides, we observed a wide range of dispersal distances traveled and a notable variation around the mean dispersal distance by female dyads. At the beginning of the breeding season, the dispersal distance more frequently registered for most of the female dyads was longer than at the end of that period. Contrary to our expectations, *C. musculinus* females seem to prefer dispersing longer distances in spring and shorter distances when population abundance is higher (i.e., summer and autumn).

The joint analysis of molecular and behavioral data is essential to characterize the social and genetic structure of small mammal populations (Matocq and Lacey 2004; Mabry 2014; Garcia-Navas et al. 2016). Indeed, the mating strategy of *C. musculinus* maintains an overlapping generation constantly, implying that the sample composition within each season consisted of individuals with different age classes and from different cohorts. This and the spatial clustering of related individuals (Wahlund effect) were the primary ecological contributors to the departures from HWE in our microsatellite loci.

The existence of positive SGS does not necessarily imply strong philopatry since SGS can be shaped by processes other than dispersal, such as mating behavior (Mabry 2014). An absence of significant autocorrelation in short-distance classes has been related to the social organization of some species, in which related individuals are not closely clustered, but

separated by a minimum distance (e.g., Staaen et al. 1996; Walker et al. 2008; Athrey et al. 2012). For example, Garcia-Navas et al. (2016) found that snow vole females *Chionomys nivalis* tend to stay within their maternal area leading to spatial clustering of related females and thereby high levels of SGS. In our study, *C. musculinus* females do not share their breeding space with other active females, showing no matrilineal clusters. *Calomys musculinus* females showed positive SGS suggesting that related females were established near one another during the breeding period (not significant in winter, Figure 2). In winter, the genetic structure may be possibly disrupted because surviving animals are a random sample of the population from the previous breeding season (i.e., genetic drift). SGS was larger in summer when, both, population abundance was at its highest as well as there was less available reproductive space. The extent of SGS could be explained by related females settling at different distances from their natal area, and even those that travelled far distances settled closer to the area of other relative females. During the breeding period, results suggest that some daughters of *C. musculinus* choose to settle physically close to their mother's territory (mother–daughter median dispersal distance was 27 m). Full sisters seem to settle each other closer than half-sisters, since the median dispersal distance was 200 and 1,300 m, respectively. We did not find enough data for full-sister dyads and further studies would be necessary to confirm if there is tolerance between them. Alternatively, half-sisters sharing the same father that are separated by large distances could reflect the geographic separation among the locations where they were born (see discussion about male mating excursions).

Extra-pair copulations and/or kin groups influenced SGS patterns even at a fine-geographic scale (Dubuc-Messier et al. 2012; Mabry 2014; Garcia-Navas et al. 2016). For example, females of eastern chipmunks *Tamias striatus* can bias the paternity of their offspring in favor of less related males (Bergeron et al. 2011). In snow voles *C. nivalis*, males may strategically adjust their mating effort according to mate relatedness (García-Navas et al. 2016). Another study by Mabry (2014) pointed out that brush mice *Peromyscus boylii* males would have “mating excursions,” which would decrease the SGS and increase the observed long-distance dispersal. Such behaviors appear related to the existence of inbreeding depression and/or postmating inbreeding avoidance mechanisms that should lead to selection for male dispersal (Lehmann and Perrin 2003; Garcia-Navas et al. 2016). The seasonal patterns of SGS in *C. musculus* males correspond to a random distribution of genotypes that would be related to their mating strategies. In summer (high population densities), the spacing behavior and movement distance of males (estimated by a recapture method) would be diminished because searching for females would be diminished too (Sommaro et al. 2010a, 2010b). However, in this study, we observed positive but weak SGS in summer (between 300 and 1,000 m) and a high frequency of dispersion at longer distances. This pattern suggests that the established males may travel greater distances to mate and sire offspring with distant females as a possible inbreeding avoidance mechanism. These mating excursions would allow males to increase their reproductive success by encountering receptive females and maintain high rates of multiple sires (65%) during the breeding period (Sommaro et al. 2015). The mating excursions have been observed in other mammals like the banner-tailed kangaroo rats *Dipodomys spectabilis* (Winters and Waser 2003).

The main hypotheses about the evolution and maintenance of sex-biased dispersal are inbreeding avoidance, competition by asymmetric limiting resources, and local mate competition (Lawson Handley and Perrin 2007; Henry et al. 2016; Li and Kokko 2019). Inbreeding avoidance and the 2 competition hypotheses are not mutually exclusive since a sex-biased dispersal by competition also implies weak breeding among related individuals. *Calomys musculus* is a promiscuous species, in which the dispersal patterns suggest that each sex would assess the costs and benefits of dispersing differently since the intersexual resource competition varied when the timing aspect of dispersal was considered. Females have ephemeral time to reproduce, taking advantage of at least 5 mating events with a high capacity for polyandry. In turn, the males benefit from the females' characteristic to disperse more frequently and farther, thus increasing their reproductive success.

Our study revealed that the spatial structure was not limited to island-like demes and dispersal occurred fluidly and without barriers among the trapping sites. Therefore, it is probable that some dispersal events can be missed beyond the boundaries of the study area, which would indicate secondary roads and cultivated fields do not constitute a barrier to dispersal per se. The results at fine-scale showed that *C. musculus* combines SGS and dispersal distances opposite to expected when the population abundance increases. Long-term studies would be necessary to confirm that population density influences dispersal distance or maybe settlement decisions may be influenced by the presence of conspecifics

(density-dependent dispersal hypothesis in males and females) (e.g., Aars and Ims 2000; Lucia et al. 2008; Centeno-Cuadros et al. 2011; Mabry 2014; Denomme-Brown et al. 2020; Leon et al. 2022).

To summarize, *C. musculus* individuals may gain direct and indirect benefits from dispersal. The direct benefits of philopatry versus dispersal are reflected in the resource acquisition hypothesis (breeding space for females and breeding females for males) as suggested by Steinmann et al. (2009) and Steinmann and Priotto (2011). Whereas the indirect effect of dispersal on spatial relatedness patterns in a species with multiple mating in a breeding cycle would be related to relaxing the competition in the natal area and increasing the encounter rate with individuals of the opposite sex as suggested in Li and Kokko (2019) in species with a promiscuous mating system. Our study shows the value of the genetic assessment together with fieldwork observations and behavioral data on dispersal estimation, even at a small geographical scale.

Ethics approval

At the time of the fieldwork for this study, the workplaces of the researchers responsible for this study had no Institutional Committee for Care and Use of Laboratory Animals in place, which was created in 2014 (Facultad de Ciencias Exactas Físicas y Naturales, Universidad Nacional de Córdoba RES. CDN° 571/2014) and 2019 (Universidad Nacional de Río Cuarto, RES. CSN° 376/19, Comité de Ética de la Investigación). However, as we state in the manuscript, animals were tested according to the guidelines proposed by the American Society of Mammalogists (Sikes et al. 2019) and the Argentina Law (National Law 14346).

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Conflict of interest

The authors declare that they have no conflict of interest.

Author contributions

All authors contributed to the development of the ideas in the paper. L.V.S.; J.W.P., M.B.C. and A.R.S. collected data. Laboratory was carried out by L.V.S. L.V.S. and J.J.M. performed data analysis and wrote the first draft of the manuscript. All authors contributed substantially to revisions and gave final approval for publication.

Supplementary material

Supplementary material can be found at <https://academic.oup.com/cz>.

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