



2 Contrasting patterns of natal dispersal of a south temperate House 3 Wren population at local and regional scales

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7 Abstract

8 Dispersal constitutes one of the main processes that shape population genetic structure and dynamics. Combining a capture-
9 mark-resighting methodology and molecular genetics analyses, we studied the natal dispersal behaviour of House Wrens
10 (*Troglodytes aedon bonariae*) inhabiting a naturally fragmented habitat in south temperate Argentina. Based on data collected
11 over 12 breeding seasons (2005–2016), we tested if males and females differ in natal dispersal behaviour at different spatial
12 scales. At local scale (within study sites), both resighting of banded individuals and genetic analysis showed that females
13 dispersed greater distances than males. At a broader spatial scale (between study sites) resighting of banded individuals could
14 not verify that females were the dispersing sex since long-distance dispersal was rare. However, genetic analyses revealed
15 paradoxical evidence: while the females of populations separated by more than 5 km showed slight but significant genotypic
16 differences among them, males showed genetic differences at a greater distance (> 16 km). Given that genetic analyses can
17 provide evidence of both historical and present-day dispersal the observed genetic differentiation does not necessarily imply
18 that the sex dispersal pattern is reversed at a regional scale. We propose that females have a higher probability of acquiring a
19 partner/territory at closer distances due existing male-biased population sex ratio caused but higher female mortality. Also,
20 although males are less likely to disperse, when they do, they must travel greater distances to find a suitable territory or mate.
21 Such movements would prevent the occurrence of genetic differences among male populations.

22 **Keywords** Sex biased dispersal · Spatial genetic structure · Population dynamics · Capture-mark-resighting

23 Zusammenfassung

24 **Gegenläufige Muster im Dismigrationsverhalten auf lokaler und regionaler Ebene bei einer Hauszaunkönigpopulation
25 der südlichen gemäßigten Breiten.**

26 Dismigration gehört zu den primären Prozessen, welche die genetische Struktur und Dynamik von Populationen gestalten.
27 Durch die Kombination einer Fang-Markierungs-Wiedersicht-Methodik mit molekulargenetischen Analysen erforschten wir
28 das Dismigrationsverhalten von Hauszaunkönigen *Troglodytes aedon bonariae* in einem von Natur aus fragmentierten Habitat

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29 der südlichen gemäßigten Breiten Argentiniens. Basierend auf Daten aus zwölf Brutsaisons (2005–2016) prüften wir, ob sich
 30 Männchen und Weibchen auf verschiedenen räumlichen Ebenen im Dismigrationsverhalten unterscheiden. Auf der lokalen
 31 Ebene (innerhalb der Studiengebiete) belegten sowohl die Wiedersichtungen beringter Individuen als auch die genetischen
 32 Analysen, dass sich die Weibchen über größere Entfernungen verteilten als die Männchen. Auf einer höheren räumlichen
 33 Ebene (zwischen den Studiengebieten) ließ sich durch die Wiedersichtungen beringter Individuen nicht bestätigen, dass die
 34 Weibchen das abwandernde Geschlecht sind, da Dismigration über weitere Strecken kaum vorkam. Allerdings lieferten die
 35 genetischen Analysen verblüffende Ergebnisse: Während die Weibchen von mehr als 5 km auseinanderliegenden Populationen
 36 leichte, aber signifikante genotypische Unterschiede aufwiesen, zeigten sich solche genetischen Differenzen bei den Männchen
 37 erst bei größerer Entfernung (> 16 km). In Anbetracht der Tatsache, dass genetische Analysen Belege für Dismigration sowohl
 38 in historischer als auch in heutiger Zeit liefern können, bedeutet die beobachtete genetische Differenzierung nicht automatisch
 39 auch eine Umkehr des geschlechtstypischen Dismigrationsmusters auf regionaler Ebene. Wir vermuten, dass Weibchen
 40 aufgrund eines durch höhere Sterblichkeit der Weibchen verursachten Männchen-lastigen Geschlechterverhältnisses in der
 41 Population mit größerer Wahrscheinlichkeit einen Partner/ein Revier im näheren Umkreis finden. Zwar wandern Männchen
 42 mit geringerer Wahrscheinlichkeit ab; wenn sie es aber tun, müssen sie weitere Strecken zurücklegen, um ein passendes
 43 Revier oder eine Partnerin zu finden. Derartige Wanderungen würden die Ausbildung genetischer Unterschiede zwischen
 44 Männchenpopulationen verhindern.

45 Introduction

46 Natal dispersal is defined as the movement of an individual
 47 between the site of birth and the site where it first attempts
 48 to breed (Greenwood et al. 1979; Greenwood and Harvey
 49 1982). It constitutes one of the main processes that shape
 50 population genetic structure and dynamics (Hamilton and
 51 May 1977; Johnson and Gaines 1990; Whitlock 2001),
 52 affecting multiple levels of organization, from genes to
 53 populations and even communities (Clobert et al. 2001).

54 Juvenile birds should disperse when the benefits of aban-
 55 doning the site where they fledged outweigh the costs of
 56 waiting for a breeding vacancy (Clobert et al. 2009; Bonte
 57 et al. 2012). In passerine birds, females generally are more
 58 likely to disperse and to disperse longer distances than males
 59 (Greenwood 1980; Johnson and Gaines 1990; Clarke et al.
 60 1997). Since dispersal promotes genetic exchange among
 61 populations, one likely consequence of differences in dis-
 62 persal proneness between sexes is the existence of differ-
 63 ences in the genetic population structure between males
 64 and females (Goudet 2002; Prugnolle and de Meeüs 2002).
 65 Given that females are the dispersing sex in birds, a weaker
 66 fine-scale genetic population structure among adult females
 67 than among males is expected (e.g., Double et al. 2005;
 68 Temple et al. 2006; Ortego et al. 2011; Botero-Delgadillo
 69 et al. 2017).

70 The use of molecular markers has facilitated the study
 71 of the dispersal behaviour of individuals and the dynam-
 72 ics of gene flow among populations (Koenig et al. 1996;
 73 Manel et al. 2003). However, genetic estimates of dispersal
 74 represent a combination of historical and present-day dis-
 75 persal patterns (Bossart and Prowell 1998; Whitlock and
 76 McCauley 1999). Even though capture–recapture/resighting
 77 of individuals may be spatially and temporally restricted, the
 78 study of dispersal behaviour using this method may better

reflect the current dispersal pattern (Slatkin 1985; Peacock 79
 and Ray 2001). Studies that combine both genetic data and 80
 field observations are scarce (but see Peacock and Ray 2001; 81
 Boulet et al. 2007; Coulon et al. 2008, 2010; Alcaide et al. 82
 2009; Ortego et al. 2011; Botero-Delgadillo et al. 2017), 83
 although the combination of the two methods may provide a 84
 more comprehensive representation of the spatial dynamics 85
 of a species (Coulon et al. 2008; Cayuela et al. 2018). For 86
 example, in the same population genetic studies can reveal 87
 high gene flow in the past or rare long-distance dispersal 88
 events whereas field data can show a strong philopatry and 89
 restricted dispersal (Peacock and Ray 2001; Alcaide et al. 90
 2009). 91

92 In this study, we combine capture and resighting observa-
 93 tions of banded juveniles and genetic markers to analyse the
 94 natal dispersal behaviour of south temperate House Wrens
 95 (*Troglodytes aedon bonariae*) inhabiting naturally frag-
 96 mented forests. A previous study in north temperate House
 97 Wrens (*T. a. aedon*) found that the distance of natal dispersal
 98 was similar between males and females although females
 99 had a lower return rate (Drilling and Thompson 1988). This
 100 was attributed to the low natal philopatry of the females
 101 although confirmatory data were not presented. In addition,
 102 Arguedas and Parker (2000) found that northern house wren
 103 populations did not show a genetic structuring, suggesting
 104 that migratory habits contribute to the lack of genetic dif-
 105 ferentiation of populations more than 400 km apart (F_{ST}
 106 for populations separated by > 300 km = 0.0017). In con-
 107 trast, in tropical house wren (*T. a. musculus*), these authors
 108 found a marked genetic differentiation between populations
 109 that were 25 km apart (F_{ST} for populations separated by
 110 25 km = 0.005). This difference with the northern temper-
 111 ate population was attributed to the resident status of this
 112 species in the tropics, where couples defend the territories
 113 throughout the year and reproductive dispersal movements

114 and settlement of individuals appear to be restricted by the
 115 availability of territories (Freed 1987). Similarly, south
 116 temperate House Wrens are year-round residents and their
 117 movements appear to be restricted by the availability of
 118 territories (Carro et al. 2017) which could limit gene flow
 119 between populations. However, the dispersal of juveniles
 120 once they leave the nest could be an important source of
 121 gene flow between populations contributing to the lack of
 122 genetic differentiation or structuring. Nevertheless, restric-
 123 tions on access to territories or mates for reproduction may
 124 differ between the sexes, resulting in a sex-biased pattern
 125 of dispersal (Arlt and Pärt 2008). In the south temperate
 126 house wren, males have a higher survival rate than females
 127 (Llambías et al. 2015), which may reduce the probability of
 128 access to a territory for juvenile males at the natal site, forc-
 129 ing them to disperse. Females, on the other hand, would be
 130 more likely to obtain a mate and a territory within the natal
 131 site so their restrictions to establish and breed may be less.
 132 If sex bias in dispersal exists, we can expect that the spatial
 133 genetic structure should be stronger for the most philopatric
 134 sex (Banks and Peakall 2012). Understanding the relation-
 135 ship between natal dispersal and genetic structure, both at
 136 population and sex-specific levels, will then contribute to
 137 elucidating the mechanisms of gene flow in south temperate
 138 House Wrens and the role that sex-dependent natal dispersal
 139 has on the degree of genetic differentiation. Specifically, we
 140 assess in this study whether there is a restriction on natal dis-
 141 persal in House Wrens populations in a naturally fragmented
 142 habitat, and whether this restriction generates different pat-
 143 terns of genetic structuring between the sexes.

144 Methods

145 Study species

146 The House Wren is a small (11–13 g), short-lived insecti-
 147 vorous passerine that inhabits open and semi-open wood-
 148 lands from southern Canada to southern Argentina and Chile
 149 (Brewer 2001). House Wrens breed in tree cavities or holes
 150 excavated by other bird species but readily use nest-boxes
 151 when available (Johnson 2014).

152 At our study site, House Wrens are residents, breed
 153 from October to early January (Llambías and Fernández
 154 2009). Both sexes exhibit high breeding site philopatry
 155 (Carro et al. 2017) and males defend small ($\approx 710 \text{ m}^2$),
 156 multi-purpose territories year-round where females settle
 157 (Llambías et al. 2015; Carro et al. 2017). Males often com-
 158 pete not only to attract females but also to usurp a territory
 159 where a female is already settled (Llambías 2012). The
 160 few cases of polygyny detected in these populations were
 161 due to territory take-over (Llambías 2012). Only females
 162 incubate the eggs and brood the young, but both, males

163 and females feed the nestlings (Fernández et al. 2012; Lla-
 164 mbías et al. 2015). Females lay 3–7 eggs per clutch (mean:
 165 4.85) and incubate the eggs for approximately 15 days
 166 (Llambías and Fernández 2009; Llambías et al. 2015).
 167 Nestlings usually fledge synchronously approximately
 168 17 days after hatching (Llambías and Fernández 2009;
 169 Llambías et al. 2015). After the nestlings of the first brood
 170 have fledged, approximately 40% of the females will lay
 171 a second clutch (Carro et al. 2014; Llambías et al. 2015).
 172 The predominant mating system is social monogamy with
 173 moderate rates of divorce and extra-pair paternity (LaBar-
 174 bera et al. 2010; Carro et al. 2017).

175 Study site

176 We studied the natal dispersal of House Wrens breed-
 177 ing in nest-boxes for a 12-year period (2005–2016) in
 178 an 8-ha South Temperate woodland (LE; Fig. 1) near the
 179 town of General Lavalle, Buenos Aires province, Argen-
 180 tina ($36^\circ 28' \text{ S}$, $56^\circ 58' \text{ W}$). The study site is located in
 181 a highly heterogeneous landscape characterized by natu-
 182 rally fragmented woodlands (composed mainly of *Celtis*
 183 *ehrenbergiana*, *Scutia buxifolia* and *Schinus longifolius*)
 184 in the so-called flooding Pampas (Vervoost 1967). Wood-
 185 land fragments occupy less than 1% of land and woodland
 186 patches rarely exceed 10 ha, and are surrounded by grass-
 187 lands and agricultural fields (Lacoretz 2018).

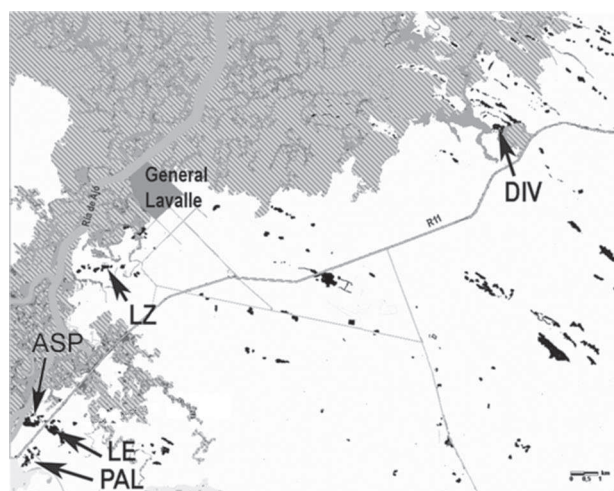


Fig. 1 Map of the study area. Forest fragments are shown in black, indicating populations sampled with an arrow, areas flooded by the tides in gray and grassland matrix in white. LE corresponds to the main study area. LZ, ASP and PAL corresponded to woodland patches where we searched for banded juveniles. LE, LZ and DIV area woodland patches where we captured and bled individuals to perform genetic analysis

188 **Field methods**

189 We installed most of the nest-boxes ($n = 93$) at LE in 2005;
190 however, a small proportion of boxes ($n = 19$) were added
191 later during the study period. House Wrens bred in more
192 than 95% of cases in the nest-boxes since 2005, which ena-
193 bled the surveillance of most dispersal events (Carro et al.
194 2017).

195 About 87–95% of the reproductive adults were captured
196 every year and marked with a combination of an aluminium
197 and three plastic colour bands. Most unbanded individuals
198 were captured using mist-nets early in the breeding season,
199 before the first-breeding attempt. However, a small propor-
200 tion of wrens were captured inside the nest-box when feed-
201 ing 10–12 days old nestlings, with a manually triggered wig-
202 wag trap (<http://golondrinas.cornell.edu/>). These unbanded
203 individuals were assumed to be juvenile immigrants that
204 joined the population (migrant recruited). Since not all indi-
205 viduals in the population were captured and banded each
206 year, a small percentage of resident individuals may have
207 been included in the estimation of the immigrants recruited.
208 Adults were sexed using external morphological traits (pres-
209 ence of brood patch or cloacal protuberance) and singing
210 behaviour (only males sing complex songs) (Lowe 1989;
211 Ralph et al. 1993).

212 We checked nest-boxes at LE every 2–3 days and on daily
213 basis when females were close to laying, eggs were close to
214 hatching or nestlings were near fledging. We marked nest-
215 lings when they were 10 days old with a single numbered
216 aluminium band. During nest checks, we opportunistically
217 recorded singing perches, agonistic behaviour and resighted
218 banded individual while foraging and nest-building to define
219 territory boundaries.

220 We monitored four additional study sites to evaluate natal
221 dispersal at a regional scale, (Fig. 1). During 2005–2012,
222 we resighted wrens in a population breeding in nests-boxes
223 at LZ (5.2 km away from LE) where both adults and fledg-
224 lings were banded (see detailed description of the study site
225 and field procedures in Llambías et al. 2015). We resighted
226 wrens breeding in tree cavities in other two sites, ASP
227 (0.7 km from LE) during 2008–2010, and PAL (0.9 km from
228 LE) during 2009 and 2010 (Fig. 1). When we detected an
229 individual marked with an aluminium band, it was recap-
230 tured and marked with three additional plastic colour bands.

231 We obtained blood samples from the brachial vein dur-
232 ing 2007 and 2008 from 36 individuals (18 males and 18
233 females) at the main study area (LE), 27 individuals (16
234 males and 11 females) at LZ and 20 individuals (18 males
235 and 2 females) at another site (DIV) 16.8 km away from LE
236 and 13.3 km from LZ (Fig. 1). Blood samples (20–40 μ l)
237 were stored in lysis buffer (100 mM Tris [pH 8.0], 100 mM
238 EDTA, 10 mM NaCl, 1% sodium dodecyl sulphate; Long-
239 mire et al. 1988). At DIV, wrens were only marked with an

aluminium band while at LE and LZ individuals were also
colour-banded. 240 241

Field data analyses 242

To assess differences in natal dispersal between sexes in
LE, we used a generalized linear mixed model (GLMM) with
the number of aluminium-banded males and females recruited
each year as the response variable, sex as a predictor, and
breeding season (year) as a random variable. We also in-
cluded the log of the total number of individuals recruited
each year (assumed to be the total number of estimated im-
migrants recruited at the beginning of each breeding season
+ the number resighted of aluminium-banded individuals) as
an offset. For this analysis, we assumed a Poisson error dis-
tribution and we used a log link function. 243 244 245 246 247 248 249 250 251 252 253

We also compared the dispersal distance between males
and females within LE, calculating this distance as the Eu-
clidean distance from the hatching nest-box to the first-
breeding nest-box (Greenwood and Harvey 1982). Only 1
year-old juveniles (84.6% of the total of banded juveniles
resighted) were included for this analysis. The differences
in dispersal distances between males and females were com-
pared using a general linear mixed model (LMM). We in-
cluded natal dispersal distance as the response variable (log
transformed to meet analysis assumptions), sex as a fixed
factor, and breeding season as a random factor. The re-
duced number of aluminium-banded individuals resighted
outside our study area (see “Results”) precluded us from
performing any statistical analysis; hence, we only present
descriptive results of dispersal between study sites. 254 255 256 257 258 259 260 261 262 263 264 265 266 267 268

Since dispersal distances can be affected by the availabil-
ity of territories or mates, the observed dispersal distances
of males and females within our study location were also
compared with simulated distributions of dispersal distances
assuming that (1) individuals occupy the nearest available
nest-box (it also included the natal nest-box if available)—a
random-walk process, or (2) individuals settle randomly in
any available nest-box within the studied plot every year -a
random process. We assumed that a nest-box was available
when it was unoccupied or was occupied by an immigrant
male or female that year. In the latter case, we assumed that
immigrant individuals compete and occupy territories after
the juveniles have settled. Therefore, we randomly assigned
a nest-box for each individual for nesting, the nest-box se-
lection only constrained by the availability for each breeding
season. Simulations under scenario 2 were repeated 100
times (under the scenario 1, the nearest available nest-box
only allowed us to make one assignment for each individual)
and results were used to estimate the expected median dis-
persal distance for each individual. We compared the dis-
tribution of observed dispersal distances and the expected
median dispersal distances assuming a random settlement 269 270 271 272 273 274 275 276 277 278 279 280 281 282 283 284 285 286 287 288 289 290

291 and the nearest settlement possible with Wilcoxon rank tests
292 for paired samples.

293 We performed all statistical modelling using the lme4
294 software package (Bates et al. 2015) running in R environ-
295 ment (R Core Team 2017).

296 Microsatellite genotyping

297 We extracted genomic DNA from blood samples using the
298 salting out procedure (Miller et al. 1988). All 109 indi-
299 viduals were genotyped using a polymerase chain reaction
300 (PCR) to identify alleles at six polymorphic microsatellite
301 loci developed specifically for House Wrens (Table 1). PCR
302 amplifications were performed in 15 µl reactions contain-
303 ing 10 ng of DNA, 5 mM MgCl₂, 1 mM dNTPs, 0.1 µM of
304 each primer, and 0.5 U Taq polymerase. PCR thermal pro-
305 files varied for each locus (Table 2). The forward primer for
306 each locus was fluorescently labelled and fragment analysis
307 was carried out on an ABI PRISM 3730 XLs DNA analyser
308 (Applied Biosystems, Macrogen).

309 Genotyping profiles (presence and allele size for each
310 locus) were scored using Peak Scanner v.1.0 software
311 (Applied Biosystems, Foster City, CA, USA). The Micro-
312 Drop Programme (Wang and Rosenberg, 2012) was used to
313 impute missing microsatellite data.

Table 1 Allele number, allele size, observed heterozygosity and number of private alleles for the five loci studied in 83 southern House Wren individuals

Locus	Allele number	Allele size (pb)	Ho	Private alleles
TA-B4 (2) ^a	10	162–184	0.75	0
TA-C3 (B)2 ^a	15	194–232	0.88	1
TA-A5-15 ^a	4	178–184	0.41	0
Pca3 ^b	5	146–160	0.49	0
ThPI-14 ^c	18	235–277	0.95	4
Overall	10.4	146–277	0.7	0

^aCabe and Marshall (2001)

^bDawson et al. (2000)

^cBrar et al. (2007)

314 We tested for departure from Hardy–Weinberg equilib-
315 rium (HWE) at each locus using Genepop v.3.1 software
316 (Raymond and Rousset 1995a). We also tested for linkage
317 disequilibrium using the Exact test based on Markov chains
318 (Raymond and Rousset 1995b) and the presence of null
319 alleles was tested using Micro-Checker v.2.2.3 software (van
320 Oosterhout et al. 2004). There was no evidence of linkage
321 disequilibrium between any pair of loci, and no significant
322 deviations from HWE were detected after applying Bonfer-
323 roni correction for multiple comparisons (all $p > 0.1$), except
324 for locus TA-A5-2 (all $p < 0.02$). Also, null alleles and a
325 highly positive F_{is} ($F_{is} > 0.30$) were detected for this locus
326 and, therefore, it was excluded in further analyses.

327 Genetic structure analyses

328 We assessed the genotypic differentiation of three study
329 plots (LE, LZ and DIV) using the modified Wright's fixa-
330 tion indices (F_{ST}) according to Weir and Cockerham (1984)
331 between pairs of populations and among all populations.
332 These computations were performed in Genepop v.3.1
333 (Raymond and Rousset 1995a). We used the program GDA
334 (Lewis and Zaykin 2001) to calculate 95% confidence inter-
335 vals around the estimated F_{ST} values with 1000 bootstrap
336 resamplings of the data.

337 Spatial genetic structure was evaluated applying spa-
338 tial autocorrelation analyses conducted in GenAlEx 6.5
339 (Peakall and Smouse 2012). Separate autocorrelations
340 were performed for the overall dataset and for males and
341 females. Analyses by sex were performed both, at local spa-
342 tial scale (within study sites, considering distances up to a
343 maximum of 900 m) and at regional scale (between study
344 sites, including comparison between LE, LZ and DIV sites
345 and testing for genetic structuration up to a maximum dis-
346 tance of 17 km). We used the UTM coordinates of sites
347 where individuals were captured to estimate geographic
348 distances. Genetic and geographical distances were used
349 to calculate multilocus genetic autocorrelation coefficients
350 (r). Under a restricted dispersal scenario, estimated r val-
351 ues should decrease with increasing geographical distance
352 between individuals. We used two approaches to assess the

Table 2 Thermal cycling processes for polymerase chain reaction (PCR) for six microsatellite loci in House Wrens

Locus	Initial denaturation	Annealing	Final elongation
TA-B4 (2)	94 °C: 3 min	95 °C: 30 s, 55 °C: 30 s, 72 °C: 30 s (35 cycles)	72 °C: 35 min
TA-A5-2	95 °C: 3 min	95 °C: 30 s, 62 °C: 30 s, 72 °C: 30 s (35 cycles)	72 °C: 15 min
TA-A5-15	95 °C: 3 min	95 °C: 1 min, 62–60 °C: 1 min, 72 °C: 1 min (20, 15 and 10 cycles)	72 °C: 40 min
ThPI-14	95 °C: 3 min	95 °C: 1 min, 62–60 °C: 1 min, 72 °C: 1 min (20, 15 and 10 cycles)	72 °C: 40 min
TA-C3 (B)2	95 °C: 5 min	95 °C: 45 s, 60–56 °C: 45 s, 72 °C: 45 s (5 cycles); 95 °C: 45 s, 55 °C: 45 s, 72 °C: 45 s (30 cycles)	72 °C: 15 min
Pca3	95 °C: 3 min	95 °C: 45 s, 62–60 °C: 45 s, 72 °C: 45 s (20, 15 and 10 cycles)	72 °C: 20 min

353 existence of spatial genetic structure. Initially we calculated
 354 r for evenly increasing spatial distances using a distance
 355 interval size of 150 m for the local scale analyses (within
 356 study sites) up to a maximum of 900 m (corresponding to the
 357 maximum inter-individual distances within the study sites).
 358 For the analyses at the regional scale (between study sites),
 359 we partitioned the geographic distances into three classes,
 360 whose upper limits were 4, 8 and 18 km, to clearly separate
 361 individuals inhabiting different study sites (Fig. 1). In
 362 addition, we estimated the representative distance that could
 363 reveal the extent of detectable positive spatial genetic structure
 364 by calculate r for increasing distant class size using the
 365 Multiple Dclass option in GenAlEx (Peakall et al. 2003).
 366 We used distances ranging from 50 m to the maximum inter-
 367 individual distance recorded for the analysis of within study
 368 site variation, and distances ranging from 1 to 17 km for
 369 the analysis of spatial variation between sites. Significance
 370 of autocorrelation values were assessed comparing the calculated
 371 r values with a 95% confidence interval (CI) built
 372 using 999 random permutations of all individuals among
 373 the geographic locations under the assumption of no spatial
 374 structure (r_p). The overall significance of the correlograms
 375 was tested using the heterogeneity test, considering it significant
 376 when $p < 0.01$ (Banks and Peakall 2012). Also, we
 377 estimated the 95% CI about observed r using bootstrap resampling
 378 1000 times. We considered that there was spatial genetic
 379 structure when: (1) the probability that the estimated
 380 r_p being greater or equal to the observed r values was less
 381 than 0.05 (Banks and Peakall 2012); (2) observed r did not
 382 lie within CI around r_p (Peakall et al. 2003); and (3) 95%
 383 CI about observed r did not include the zero value (Peakall
 384 et al. 2003). We excluded DIV from the between study sites
 385 comparison for females as we were only able to capture 2
 386 females at this site.

387 Results

388 Field observations

389 We banded a total of 1,277 fledglings in our study area
 390 during the breeding seasons of 2005–2015. Of these, 159
 391 (12.5%) were resighted defending a territory or nesting
 392 during the following breeding season after fledging (i.e.,
 393 yearlings; 108 males and 51 females) and 29 (2.27%) were
 394 resighted 2 years afterwards (i.e., 2-year-old individuals).
 395 These represented 31.7% of total number of individuals
 396 recruited (immigrants + banded juveniles) into the population
 397 during the 2006–2016 period ($n = 593$). Males banded
 398 as nestlings were more frequently recruited than females
 399 ($50.6 \pm 11.31\%$ vs. $25.8 \pm 8.02\%$, mean \pm SD; $\chi^2_1 = 23.6$,
 400 $p < 0.01$; Fig. 2). We were able to capture 89% (96/108) and
 401 76% (39/51) of these recruited banded males and females,

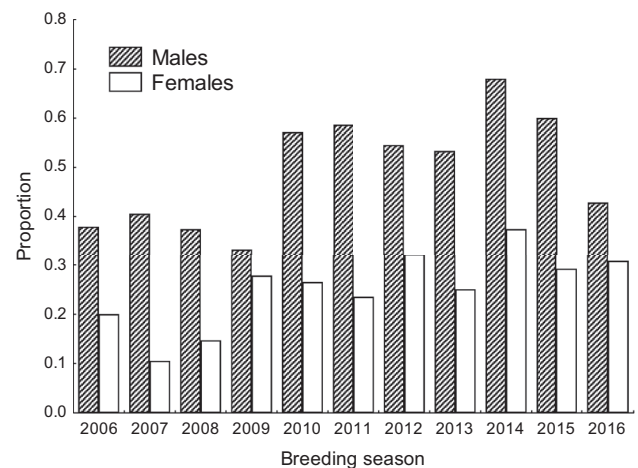


Fig. 2 Frequency of marked southern House Wren juveniles recruited at the studied population during the 2006–2016 breeding seasons

402 respectively. There were differences in the distance dispersed
 403 by males and females from their natal nest-boxes
 404 ($\chi^2_1 = 10.82$, $p = 0.001$). The median dispersal distance
 405 for males was 179.05 m (range 43.57–655.44), whereas
 406 females dispersed 262.09 m (range 73.22–626.64) (Fig. 3).
 407 Dispersed distances were larger than the distance to the
 408 nearest available nest-box for both males (Wilcoxon Rank
 409 test, $Z = 6.27$, $p < 0.001$) and females (Wilcoxon Rank
 410 test, $Z = 4.20$, $p < 0.001$). While females dispersed significantly
 411 longer distances than those expected using random simulations
 412 (Wilcoxon Rank test, $Z = 3.18$, $p = 0.002$), males did
 413 not (Wilcoxon Rank test, $Z = 0.20$, $p = 0.84$).

414 During 2008–2010 breeding seasons, we detected 14
 415 individuals (5 males and 9 females) banded as nestlings in
 416 our study site nesting in neighbouring areas (PAL and ASP;
 417 Table 3). These individuals dispersed less than 1 km. Furthermore,
 418 during the 2005–2012 period, none of marked fledglings at LE
 419 we sighted at LZ (5 km away) but we observed one female that
 420 dispersed from LZ as juvenile, nesting at LE during 2007. These
 421 observations suggest that long-distance dispersal is apparently
 422 infrequent at our study area.
 423

424 Genetic population structure

425 Allelic polymorphism varied among populations, with number
 426 of alleles (A) ranging from 7.8 to 9.8 (Table 4). We also
 427 found five private alleles (i.e., alleles that were found only
 428 in a single population; occurrence range 0.02–0.08). Four of
 429 these alleles were found at LE, whereas the remaining private
 430 allele was found in DIV. Allelic richness (A_p) was similar
 431 among populations averaging 6 (Table 4). Observed and
 432 expected heterozygosity were equivalent across populations.

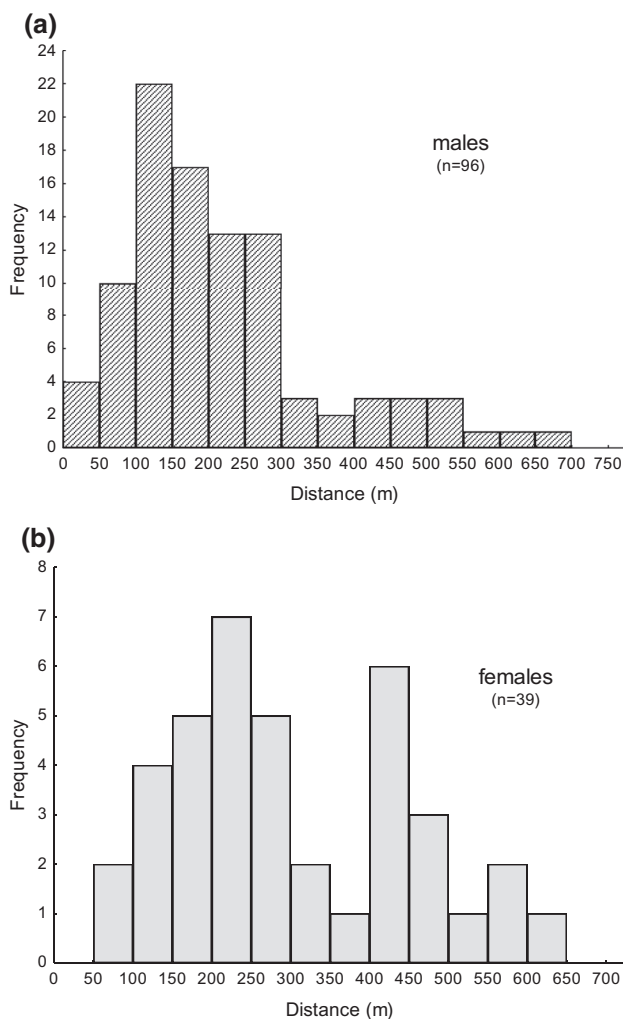


FIGURE 3

Fig. 3 Natal dispersal distances for southern House Wren males (a) and females (b) during 2005–2016. Individuals were marked at nests as fledglings and resighted and captured in the following breeding season as reproductive adults

Table 3 Number of individuals marked as fledglings in LE resighted in neighbouring sites the following breeding season

Year	PAL		ASP		LZ		LE	
	Males	Females	Males	Females	Males	Females	Males	Females
2008	–	–	0 <i>n</i> =17	0 <i>n</i> =5	0 <i>n</i> =32	0 <i>n</i> =27	15 <i>n</i> =57	5 <i>n</i> =35
2009	4 <i>n</i> =24	2 <i>n</i> =11	0 <i>n</i> =26	2 <i>n</i> =15	0 <i>n</i> =21	0 <i>n</i> =21	4 <i>n</i> =37	4 <i>n</i> =24
2010	1 <i>n</i> =19	4 <i>n</i> =9	0 <i>n</i> =40	1 <i>n</i> =18	0 <i>n</i> =35	0 <i>n</i> =32	16 <i>n</i> =43	9 <i>n</i> =38

PAL and ASP correspond to woodland patches less than 1 km away; LZ is 5.2 km away from LE. We also indicated the number of individuals banded as fledglings at LE that remained at the study area the following breeding season. *n* represents the total number of individuals of each sex sighted at each site

Ho and He averaged ≈ 0.7 (Ho range = 0.63–0.73; He range = 0.67–0.76; Table 5).

F_{ST} values between pairs of populations varied between 0.007 and 0.013 (Table 6). Although F_{ST} values were low, populations that were separated by more than 5 km had the highest values ($F_{ST} > 0.01$, exact test p values < 0.05). When sexes were analysed separately, genotypic differences between LE and DIV—separated by ~ 16 km—were only detected for males. No statistically significant differences were found between male populations between LE and LZ (Table 6). In contrast, females did show marked genotypic differences between the nearest populations: LE and LZ (Table 6).

Spatial genetic autocorrelations

Local scale (within study sites)

Genetic autocorrelation r coefficients for complete dataset increased with the distance class size departing significantly from random expectations when distance interval was 150 m, and then decreasing for intervals > 200 m where r is not significantly different from zero (Fig. 4a). Similarly, autocorrelation analysis using 150 m distance intervals showed that individuals were nonrandomly distributed in space ($\omega = 32.29$, $p < 0.01$; Fig. 5a). The r value was positive and differed significantly from random only at small distances (150 m), and then, decreasing for distances > 150 m and not departing from expected randomness (Fig. 5a). Males showed a similar pattern of genetic structuration ($\omega = 39.65$, $p < 0.01$), with closer individuals (< 150 m) being more related than expected by chance (significantly positive r values; Figs. 4b, 5b). In contrast, autocorrelation values for females did not reveal an evident genetic structuration, with r values not differing from those expected at random ($\omega = 12.22$, $p = 0.42$; Figs. 4c, 5c).

Table 4 Microsatellite diversity for three southern House Wren populations across five loci

Site	Loci						A_r
	<i>TA-B4 (2)</i>	<i>TA-C3 (B)2</i>	<i>Pca3</i>	<i>ThPl-14</i>	<i>TA-A5-15</i>	A	
LE	10	13	6	16	4	9.8	6.4
LZ	6	13	5	13	4	8.2	5.8
DIV	9	11	4	12	3	7.8	5.8

Number of individuals sampled were: 36 at LE, 27 at LZ and 20 at DIV

A average number of alleles per locus, A_r allelic richness

Table 5 Observed (H_o) and expected heterozygosity (H_e) and number of alleles per population (A) estimated for different southern House Wren populations

Site	H_o	H_e	A	Patch area (ha)
LE	0.73	0.76	49	14.60
LZ	0.63	0.69	41	10.56
DIV	0.71	0.67	39	13.58
Average	0.69	0.71		

Patch area (ha) is indicated for each population

466 Regional scale (between study sites)

467 Local populations (inter-individual distances < 4 km)
 468 were more related than expected by chance, decreasing
 469 r with distance ($\omega = 26.01$, $p < 0.01$; Fig. 6a). Genetic
 470 autocorrelation for increasing distance class size also
 471 revealed positive and significant r values up to 5 km
 472 (Fig. 7a). Males showed a decreased genetic similarity
 473 with increased distance between individuals but it not dif-
 474 ferred from that expected by chance ($\omega = 13.95$, $p = 0.06$;
 475 Figs. 6b, 7b). In contrast, females separated by less than
 476 5 km were more closely related than expected by chance,
 477 revealing a clear genetic structure ($\omega = 22.09$, $p < 0.01$;
 478 Figs. 6c, 7c). In the traditional correlogram, we observed
 479 that females distanced between 4 and 8 km showed a sig-
 480 nificant and negative r value, indicating strong divergence
 481 and confirming the continuous cline (Fig. 6c).

Table 6 Wright's fixation indices (F_{ST}) assessing the genotypic differentiation between pairs of southern House Wren populations

Distance (km)	LE-LZ	LZ-DIV	LE-DIV
	5.2	13.3	16.8
Overall data set	0.0075 (-0.004 to 0.022)	0.013 (-0.004 to 0.036)	0.010* (0.002 to 0.019)
Males	0.002 (-0.012 to 0.02)	0.012 (-0.006 to 0.026)	0.014* (0.006 to 0.023)
Females	0.040* (0.009 to 0.074)	-	-

Confidence intervals calculated for estimated F_{ST} are presented in parentheses

* $p < 0.05$

Discussion

Capture-resighting data and population genetic analyses provide evidence of restricted natal dispersal in south temperate House Wrens at our study area. While both field observations and genetic analyses confirmed that females dispersed greater distances within study sites at local scale, genetic analyses between study sites suggest that movement of females might be more restricted at a larger spatial scale.

House Wren juveniles rarely dispersed outside of the forest patch where they fledged; we only resighted banded juveniles at forest patches less than 1 km from our main study site (LE). Accordingly, we found low but significant genetic differentiation between sites separated by more than 5 km, suggesting reduced gene flow among populations. Autocorrelation genetic analyses also showed decreased genetic relatedness among individuals as geographic distance increase. A previous study in Costa Rica found that populations of tropical House Wrens were genetically different when separated for more than 25 km (Arguedas and Parker 2000). As far as we know, our findings are the first to reveal an even finer scale genetic structure within the House Wren complex.

Restricted gene flow at small spatial scales suggests the existence of environmental and behavioural constraints in the movements of individuals (Nathan et al. 2008; Matthysen 2012). Studies focusing on Neotropical resident passerines have found genetic differentiation among populations at local scales, even among sites in continuous habitats (Barrowclough 1980; Hackett and Rosenberg 1990; Brawn and Robinson 1996; Brumfield and Capparella 1996; Bates 2000; Burney and Brumfield 2009; Woltmann et al. 2012;

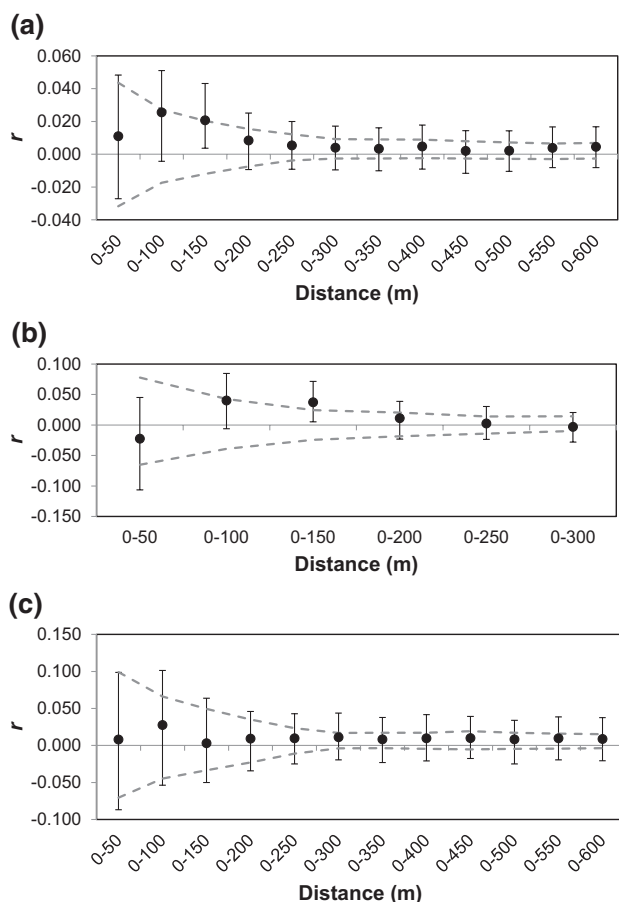


Fig. 4 Spatial genetic autocorrelation coefficients (r) for increasing distance class size at local scale (within study sites) for all individuals (a), males (b) and females (c) of the southern House Wren inhabiting three different woodland patches (LE, LZ and DIV). Dots represent correlation coefficients and bars are the 95% confidence intervals estimated by bootstrapping. Dashed lines indicated the upper and lower limits of the confident intervals for r values calculated assuming a random distribution of genotypes

513 Klauke et al. 2016). In most of these tropical species, genetic
 514 structure at such fine spatial scale has been attributed to the
 515 sedentary lifestyle (reduced mobility) and high habitat special-
 516 ization (e.g., Burney and Brumfield 2009; Khimoun et al.
 517 2016; Menger et al. 2017). Accordingly, it has been pro-
 518 posed that the genetic differences in tropical House Wrens
 519 inhabiting forests in Costa Rica are the consequence of a
 520 sedentary lifestyle (Arguedas and Parker 2000). However,
 521 sedentary lifestyle by itself may not generate an a priori
 522 fine-scale genetic structure in habitat generalists such as
 523 the House Wren (Johnson 2014). South temperate House
 524 Wrens occupy a wide range of habitats including montane
 525 woodlands, modified landscapes and arid regions with dry
 526 woodlands (Kroodsma and Brewer 2005). Furthermore, at
 527 out study site, translocation of territorial males revealed that
 528 male House Wrens are capable of flying through unsuitable

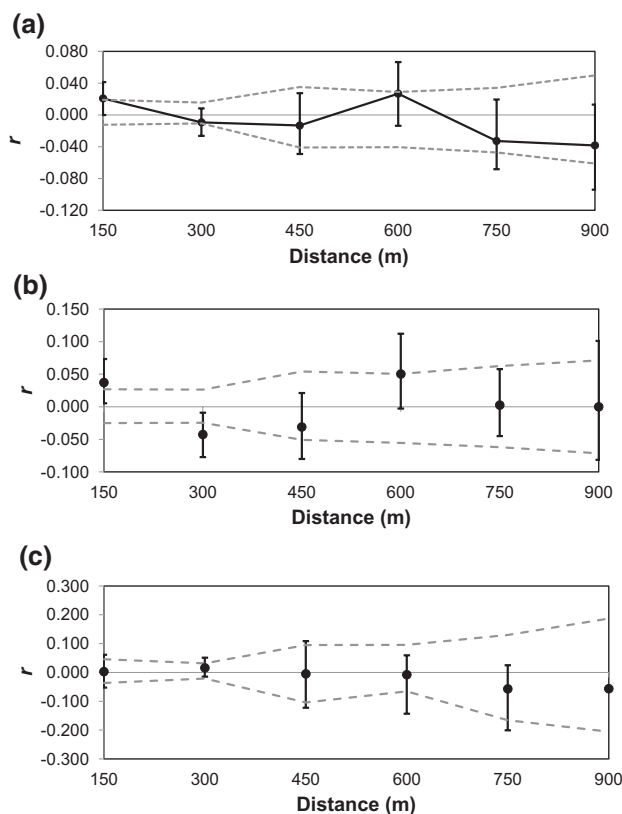


Fig. 5 Genetic correlation coefficients (r) variation as a function of the increasing distance within study sites (local scale) for pairs of all individuals (a), males (b), and females (c) of the southern House Wren inhabiting. Dots represent correlation coefficients and bars are the 95% confidence intervals estimated by bootstrapping. Dashed lines indicated the upper and lower limits of the confident intervals for r values calculated assuming a random distribution of genotypes

529 environments such salt marshes to return to their territories
 530 (P. Llambías, unpublished data). Given the flying capabil-
 531 ity and lack of habitat specialization of House Wrens, it is
 532 surprising that natal dispersal is restricted in our study area.
 533 It is possible that the fragmented nature of woodlands at
 534 our study site imposes restrictions to dispersal of individu-
 535 als. In our study area, less than 5% of the surface is covered
 536 by natural and forestry plantations, and woodland patches
 537 are separated by wide grasslands and marshes (Fig. 1).
 538 Fragmented habitats may severely limit individual disper-
 539 sal among populations increasing the costs for individual
 540 mobility through unsuitable habitats (Endler 1977; Fahrig
 541 and Merriam 1994; Frankham et al. 2002; Coulon et al.
 542 2010; Adams and Burg 2015; van Oosten et al. 2016). Gap
 543 width can have a strong effect on the ability of birds to move
 544 among patches. Wide gaps may affect the mortality of indi-
 545 viduals when dispersing but may also constitute a percep-
 546 tual constraint for birds (Ibarra-Macias et al. 2011; Awade
 547 et al. 2017). These constraints could at least partly explain
 548 the limited dispersal observed in this marked fragmented

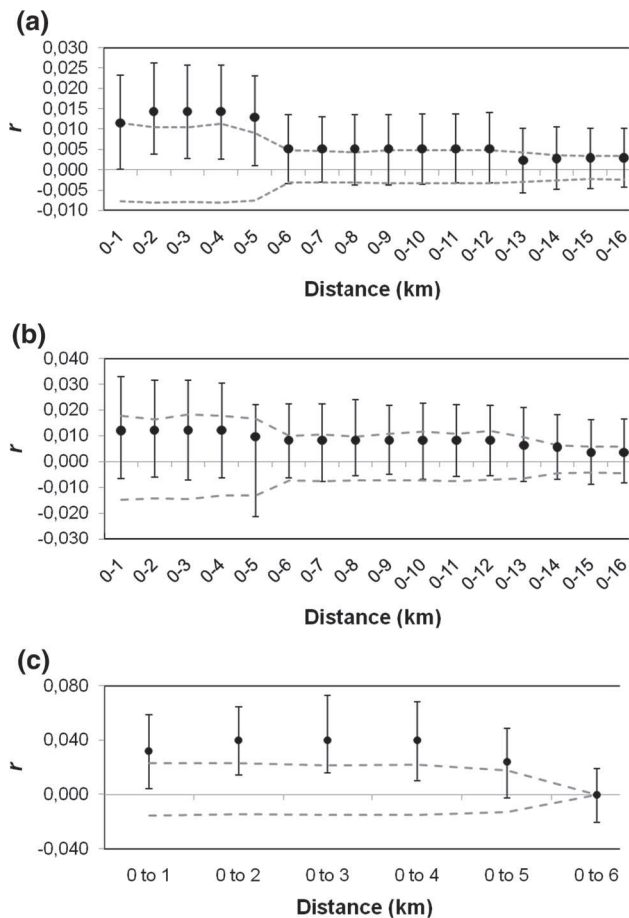


Fig. 6 Spatial genetic autocorrelation coefficients (r) for increasing distance class size at regional scale (among study sites) for all individuals (a), males (b) and females (c) of the southern House Wren. Dots represent correlation coefficients and bars are the 95% confidence intervals estimated by bootstrapping. Dashed lines indicated the upper and lower limits of the confident intervals for r values calculated assuming a random distribution of genotypes

549 landscape. Such constraints could even vary between sexes, 550 thus explaining the differences found in the House Wren. 551 Further studies comparing fragmented and unfragmented 552 habitats are necessary to clarify the effect of landscape on 553 dispersal in resident House Wrens.

554 In a previous study, we provided field evidence that 555 breeding adults were highly philopatric, with no records of 556 breeding individuals leaving the forest patch to settle in a 557 new breeding site (Carro et al. 2017). Therefore, most of the 558 gene flow must be consequence of juvenile dispersal. In our 559 study, we found sexual differences in dispersal proneness 560 of juveniles. At a local scale (within study sites), juvenile 561 females dispersed farther away from their fledging site than 562 juvenile males. This local dispersal pattern differed from the 563 one expected by chance or from that expected if individuals 564 select the nearest available nest-box. Genetic autocorrelation 565 analyses at local scale revealed a decreased relationship

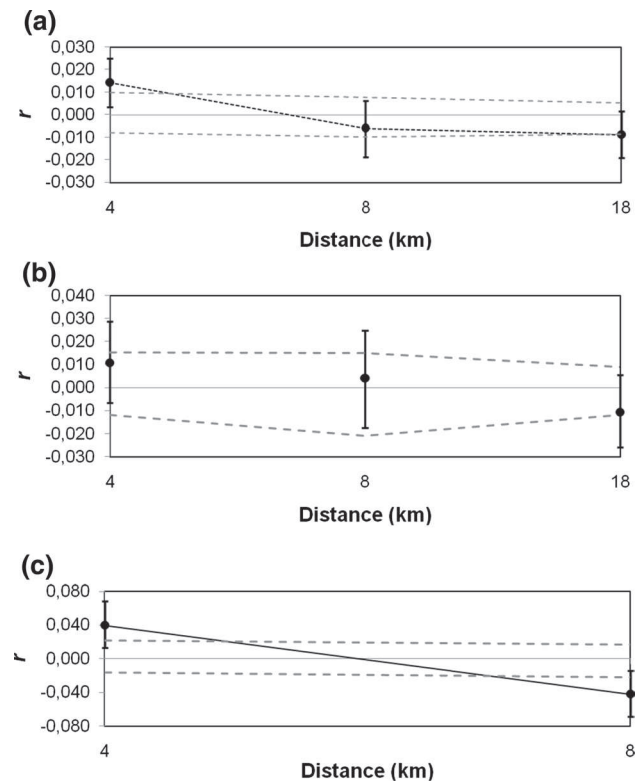


Fig. 7 Genetic correlation coefficients (r) variation as a function of the increasing distance among study sites (regional scale) for pairs of all individuals (a), males (b), and females (c) of the southern House Wren. Dots represent correlation coefficients and bars are the 95% confidence intervals estimated by bootstrapping. Dashed lines indicated the upper and lower limits of the confident intervals for r values calculated assuming a random distribution of genotypes

among males with distance but not among females, con- 566 firming this pattern. The mechanisms underlying sex-biased 567 dispersal could be manifold. Males may be reluctant to dis- 568 perse to unfamiliar areas due to the high costs associated 569 with establishing a territory with no previous information on 570 habitat quality, social interactions with neighbours and terri- 571 tory availability (Greenwood 1980; Payne and Payne 1993; 572 Winkler et al. 2005). The fact that some males returned to 573 their territories after translocation experiments (see above 574 and Kendiegh 1941) suggests that the benefits of habitat and/ 575 or neighbour familiarity are high. On the other hand, females 576 may disperse farther away than males to locate a preferred 577 male and/or territory and ultimately, reducing the long-term 578 costs of inbreeding (Greenwood 1980; Handley and Perrin 579 2007; Arlt and Pärt 2008). 580

Field records of banded individuals did not allow us to 581 determine the presence of a short-term female sexual bias in 582 dispersal at a regional scale between studied sites due to the 583 reduced number of resighted juveniles in neighbouring pop- 584 ulations. However, in our study population (LE), the recruit- 585 ment of a higher number of migrant females (unbanded 586

587 individuals) than males and of more banded juvenile males
 588 than banded juvenile females suggest that a female bias in
 589 dispersal occurs at between-sites level. However, genetic
 590 analyses provided contrary information: while female popu-
 591 lations distanced for more than 5 km reveal weak but sig-
 592 nificant genetic differentiation, males only showed genetic
 593 differentiation at greater distances (\hat{c} 16 km). Given that
 594 genetic analyses can provide evidence of both historical
 595 and present-day dispersal (Bossart and Prowell 1998), the
 596 observed genetic differentiation does not necessarily imply
 597 that the sex dispersal pattern is reversed at a regional scale.
 598 Females may still be the predominantly dispersing sex, but
 599 the observed genetic structure may be the consequence of a
 600 long-term, spatially restricted dispersal. In contrast, the lack
 601 of genetic differentiation between males may indicate that
 602 less frequent, long-distance movements occur more often
 603 among males than females. In this sense, what may explain
 604 the differences in dispersal distances between males and
 605 females is the availability of territories and/or social mates.
 606 Some studies have found that the movements of males and
 607 females may be conditioned by demographic variables. For
 608 example, Greenwood et al. (1979) found that natal disper-
 609 sal in Great Tits (*Parus major*) was related to population
 610 density, with females moving shorter distances and males
 611 moving longer distances when density is high due to greater
 612 competition for territories among males than females. Dele-
 613 strade et al. (1996) also found in this species that male and
 614 female dispersal distances did not vary with local densities,
 615 but males which changed habitat settled in areas with low
 616 occupation rates. In southern House Wren populations, the
 617 lower survival probability of adult females (Llambías et al.
 618 2015) and the adult male-biased sex ratio (Carro et al. 2017)
 619 increases the probability for females of acquiring a suitable
 620 territory and/or social partners to breed in closer populations
 621 while males may be forced to disperse over greater distances
 622 to locate a vacant territory. Alternatively, the observed dif-
 623 ferences in genetic structuring of males and females may
 624 be generated by differential mortality of juveniles. Thus,
 625 females may be dispersing over long distances but may suf-
 626 fer higher mortality than males in doing so. The cause of this
 627 differential mortality is unclear. Some studies suggest that
 628 the heterogametic sex may be more susceptible due to the
 629 expression of sex-linked deleterious recessive alleles (Triv-
 630 ers and Willard 1973; Myers 1978) predisposing them to
 631 higher mortality or reduced performance during develop-
 632 ment. However, evidence in support of this hypothesis is
 633 scarce in birds (Jones et al. 2009; Tarwater et al. 2011). It
 634 has also been found in dimorphic species that larger sexes
 635 may show higher mortality earlier in life, although in other
 636 cases, the size of individuals may be an indicator of their
 637 competitive ability with conspecifics (Husby and Slags-
 638 vold 1992; Råberg et al. 2005). However, evidence for the
 AQ4 existence of this mortality bias between sexes is scarce and

640 inconclusive (see Maness and Anderson 2013 for a review).
 641 In House Wrens, there are no data to suggest the existence
 642 of a sex bias in juvenile mortality, although this possibility
 643 cannot be totally ruled out. Further studies are necessary to
 644 unravel the effect of demographic and social effects on male
 645 and female House Wren dispersal behaviour.

646 In conclusion, our field records indicate that most indi-
 647 viduals are philopatric or disperse over short distances once
 648 they leave the nest. However, our integrative approach using
 649 molecular data also allowed us to identify long-distance dis-
 650 persal events that reduced the genetic differentiation among
 651 populations, particularly among males. The combination of
 652 the two methods provided us with complimentary informa-
 653 tion that enabled a more comprehensive understanding of
 654 dispersal behaviour of the House Wren.

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670 Declarations

671 **Conflict of interest** The authors declare no conflict of interest.

672 **Ethical statement** All methods used in the present study met the ethical
 673 requirements for science research and complied with the current laws
 674 of the country in which they were performed. This study and protocols
 675 we used were approved by the Dirección de Áreas Protegidas y Con-
 676 servación de la Biodiversidad (Disp. 44 and 91) and the Organizaci-
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 678 province, Argentina (Disp. 019/15).

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