

# Mate and territory availability affect breeding dispersal and divorce in a resident Southern House Wren *Troglodytes aedon musculus* population

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Breeding dispersal is the movement of an individual between breeding attempts and is usually associated with the disruption of the social pair bond, although mates may disperse together as a social unit. In monogamous territorial species, the decision to disperse may be affected by individual attributes such as sex, age and condition of the disperser. However, environmental and social contexts may also play a crucial role in the decision to disperse. We analysed capture-resighting data collected over 9 years to study breeding dispersal and divorce rates of a Southern House Wren *Troglodytes aedon musculus* population in South Temperate Argentina. Between-season dispersal was more frequent than within-season dispersal, with females dispersing more often than males, both between and within seasons. Both within-season and between-season breeding dispersal probability was affected by territory availability, but not by previous breeding success. When the adult sex ratio (ASR) was more skewed towards males, male between-season dispersal was also affected by mating status, with widowed and single males dispersing more often than paired males. Within-season divorce increased the reproductive success of females but not males, and was affected by the availability of social partners (with increasingly male-skewed ASR). Our results suggest that territorial vacancies and mating opportunities affect dispersal and divorce rates in resident Southern House Wrens, highlighting the importance of social and environmental contexts for dispersal behaviour and the stability of social pair bonds.

**Keywords:** adult sex ratio, breeding success, dispersal behaviour, pair bond.

Breeding dispersal is the movement of an individual or a mating pair from one breeding site to another following a reproductive attempt, within the same or different breeding seasons (Greenwood & Harvey 1982, Clobert *et al.* 2001). After a breeding event, a socially monogamous pair can breed again together (re-unite) or they can breed with a different partner (divorce; Choudhury 1995, Black 1996). Although strong philopatry may force mate-retention, breeding dispersal can strongly affect divorce rates, as it reduces the probability of re-encounter (Freed 1987, Mock &

Fujioka 1990, Cézilly *et al.* 2000, Cockburn *et al.* 2003, Gill & Stuchbury 2006, Llambías *et al.* 2008).

Both breeding dispersal and divorce have often been regarded as reproductive strategies that enable individuals to increase their reproductive success (Coulson 1966, Ens *et al.* 1996, García-Navas & Sanz 2011, Culina *et al.* 2015). In monogamous territorial species, breeding dispersal and divorce can be affected by individual and environmental factors such as sex, age, body condition, breeding success and food abundance (Greenwood & Harvey 1982, Drilling & Thompson 1988, Stamps 2001, Stamps *et al.* 2005, Ward & Weatherhead 2005, García-Navas & Sanz 2011,

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Martin *et al.* 2014, Terraube *et al.* 2015). Ultimately, the individual decision to disperse and/or divorce should be constrained by the availability and quality of alternative territories and social partners (Newton & Marquiss 1982, Pärt & Gustafsson 1989, Drilling & Thompson 1991, Choudhury 1995, Ens *et al.* 1996, Poirier *et al.* 2003, Ward & Weatherhead 2005, Blakesley *et al.* 2006, Liker *et al.* 2014). Low population densities and reductions in population density should promote both greater breeding dispersal and divorce rates, as they increase the availability of unoccupied high- to medium-quality territories (Komdeur *et al.* 1995, Paradis *et al.* 1998, Kokko & Rankin 2006). Furthermore, in socially monogamous species a skewed adult sex ratio (ASR) can destabilize pair bonds and induce divorce, as it increases mate availability for the rarer sex (Liker *et al.* 2014, Székely *et al.* 2014).

Most studies on passerines that have evaluated the factors that affect individual decisions to disperse and/or divorce have been undertaken on species of the North Temperate Zone (Greenwood & Harvey 1982, Clarke *et al.* 1997, Newton 2001). However, differences in environmental conditions, demography and life-history strategies of Tropical and South Temperate passerines suggest that they may face a different set of trade-offs that can potentially affect individual decisions (Greenberg & Gradwohl 1997, Morton *et al.* 2000, Stutchbury & Morton 2001, Macedo *et al.* 2008). Whereas in North Temperate species, a migratory lifestyle may cause asynchronous arrival on the breeding grounds, subsequently producing high divorce rates (the 'musical chair' hypothesis; Dhondt & Adriaensen 1994), the resident lifestyle coupled with high habitat saturation in the Neotropics reduces breeding vacancies and constrains dispersal and divorce strategies (Ashmole 1963, Ricklefs 1980, Freed 1987, Russell & Rowley 1996, Stutchbury & Morton 2001, but see Morton *et al.* 2000, Fedy & Stutchbury 2004).

The House Wren *Troglodytes aedon* complex is an excellent system in which to study dispersal and divorce; along its distribution range from Cape Horn to Canada, House Wrens inhabit North Temperate, South Temperate and Tropical environments, showing geographical variation in year-round residence, mating systems, song performance and life-history strategies (Freed 1986, Young 1994, Llambías *et al.* 2012, 2015, Kaluthota *et al.* 2016). In Northern House Wrens

*Troglodytes aedon aedon*, mate switching and dispersal seem to be associated with high mate availability facilitated by social polygyny and brood desertion (Drilling & Thompson 1991). In contrast, dispersal and divorce in Tropical House Wrens appear to be constrained by habitat saturation and long-term social monogamy coupled with low rates of brood desertion (Freed 1987). Here, we report data on within- and between-breeding dispersal and divorce rates in a socially monogamous, year-round resident population of Southern House Wrens *T. a. musculus* in temperate eastern Argentina. We assessed the reproductive consequences of dispersal and divorce strategies.

In assessing factors affecting dispersal and divorce decisions, we were interested in testing life history and ecological processes separately, rather than the interaction between them. Initially we assessed whether individual decisions were dependent on the age and gender of individuals. We then evaluated how male and female decisions were affected by ecological conditions such as nesting success and territory or mate availability.

## METHODS

### Study species

The House Wren is a small, short-lived, insectivorous secondary cavity-nesting passerine distributed from Canada to Tierra del Fuego (Johnson & Poole 2014, Remsen *et al.* 2015). Northern House Wrens inhabit North America, are mainly migratory (Brewer 2001, Johnson & Poole 2014) and have moderate rates of social polygyny and extra-pair fertilizations (Johnson *et al.* 1993, Soukup & Thompson 1997, Dubois *et al.* 2006, LaBarbera *et al.* 2010, Llambías *et al.* 2012), whereas Southern House Wrens are distributed across Central and South America and are mainly sedentary (Brewer 2001, Johnson & Poole 2014), with low rates of social polygyny and moderate rates of extra-pair fertilizations (Freed 1987, Llambías & Fernández 2009, LaBarbera *et al.* 2012). Both sexes contribute to building the nest, and feeding and defending the young, but only females incubate the eggs and brood the nestlings (Llambías & Fernández 2009, Fernández *et al.* 2012, Llambías *et al.* 2015). Only males develop complex songs, which are used to defend or attract a female to a cavity (Rendall & Kaluthota 2013, dos Santos *et al.* 2016). Females have been reported to have lower

adult survival than males in both North and South Temperate populations (Llambías *et al.* 2015). At our study site, the breeding season extends from mid-October to mid-January and females can raise two successful broods (Llambías & Fernández 2009, Carro *et al.* 2014).

### Study site

Over a 9-year period (2004–2012), we studied a colour-ringed House Wren population breeding in nestboxes at an 8-ha South Temperate forest patch surrounded by grasslands and agricultural fields near the town of General Lavalle, Buenos Aires province, Argentina (36°28'S, 56°58'W; Fig. 1). Forest patches in the so-called flooding pampas are composed mainly of *Celtis ehrenbergiana*, *Scutia buxifolia* and *Schinus longifolius*, and are present in a naturally fragmented pattern, occupying the higher grounds in the area (Vervoort 1967).

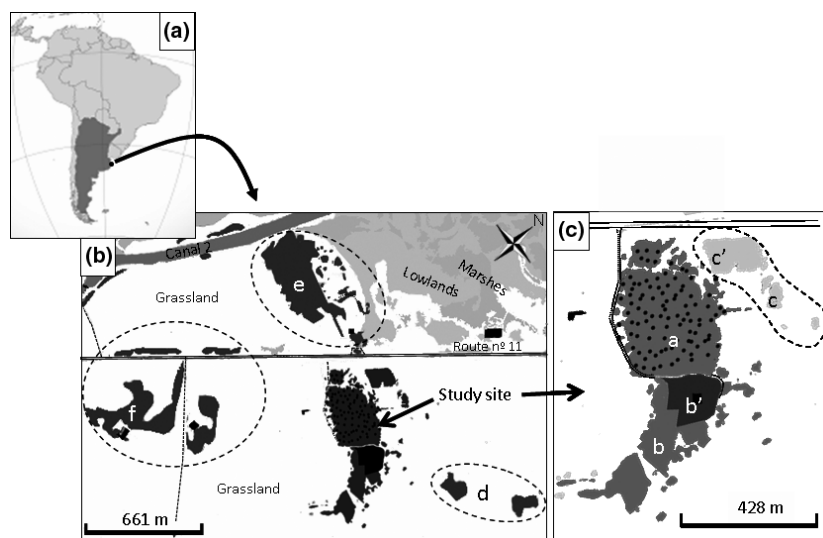
In 2004, we attached 93 nestboxes to trees at least 1.5 m above the ground. In 2012, we added 13 additional nestboxes, mainly to the periphery of the forest patch. Because of the surplus of nestboxes in our study area, breeding territories often contained more than one nestbox. Our study population bred almost exclusively (> 95%) in nestboxes, which enabled the surveillance of most

dispersal events. Once Wrens start breeding, dispersal between forest patches was minimal (see below).

### Field methods

We used behavioural observations early in the breeding season to identify ringed individuals and defined breeding territories and partnerships. During each breeding season, we mapped territories by re-sighting ringed individuals, observing each bird's movements inside the territory to define the territory's core and agonistic interactions with neighbours to define the borders. The number of territories therefore corresponded to the number of monogamous and bachelor males defending a territory. Social partners were frequently confirmed by repeatedly observing individuals defending nestboxes and provisioning nestlings.

We captured un-ringed adults before the first nesting attempt with mist-nets, attracting them with song recordings or capturing them inside the box when feeding 10- to 12-day-old nestlings. Adults were ringed with a numbered metal ring and a unique combination of three plastic colour rings. Each year, we were able to capture most un-ringed adults (87–95%). During the 2007–2010 breeding seasons, we performed regular



**Figure 1.** Location of the study site in South America (a). This corresponds mostly to a vast plain dominated by grasslands with scattered forest patches (b). In the detailed map (c), the grey areas are the forest patches studied. Areas d, e and f correspond to neighbouring forested areas checked between 2007 and 2010 for dispersing individuals. Area b was used for manipulative experiments and subsequently excluded from our analyses. Areas b', c and c' correspond to areas without nestboxes; dark spots in area a represent the approximate location of nestboxes.

censuses at four neighbouring forest patches less than 1 km apart to assess whether adults dispersed outside our study area (Fig. 1). As before, we used male song playback to stimulate male and eventually female response to identify individuals and breeding territories in these patches. Other House Wren populations remained under study by one of us (P.E.L.) in five forest patches, 5 km from our study area during the 2003–2009 breeding seasons, which allowed us to check for individual dispersal outside our study area.

Wrens were sexed using external morphological characteristics (presence of brood patch or cloacal protuberance) and behaviour (only males sing and only females incubate). We visited nestboxes every 1–3 days, and when we detected lining and feathers in the nest, we checked boxes every day to determine the exact laying date (i.e. the date when the first egg was laid). Once the nesting attempt started, we recorded clutch size (number of eggs laid), brood size (number of nestling hatched), number of young fledged and nest fate (success or failed). We ringed nestlings at nests with a unique numbered metal ring when they were 10–12 days old.

### Estimation of breeding dispersal and divorce

Breeding dispersal was defined as the movement of an individual outside its former territory to a new actively defended area and where breeding took place in a nestbox that was previously outside the territory boundaries. We only considered movements that implied the abandonment of at least 90% of the former territory and excluded the movements of individuals that expanded their territories to include additional nestboxes. We considered a within-season dispersal event to have occurred when we recorded an adult defending or nesting in two different territories between consecutive breeding attempts within the same breeding season. We considered a between-season dispersal event to have occurred when the territory defended or used for the first breeding attempt in a breeding season was different from that defended or used for the last nesting attempt in the previous breeding season.

We considered an individual to be divorced if it bred with a different social partner while the former partner was known still to be alive in the population. Similarly to dispersal, divorce can occur

between nesting attempts during the same breeding season (within-season divorce) or between breeding seasons (between-season divorce). We assumed that the individual that abandoned a territory and its partner had initiated the divorce (e.g. Cockburn *et al.* 2003, Gill & Stutchbury 2006). Because divorce is defined as the decision of one individual of the pair bond, but which affects both members of the pair, we analysed the effect of ecological factors on divorce decisions at the mating pair level.

We evaluated the variation in the probability of both within- and between-season dispersal using generalized linear mixed models (GLMMs), with individual identity and year (breeding season) as random factors. We assumed a binomial distribution of errors and used a logit link function in these models. We used a dichotomous response variable (dispersed–not dispersed) for each individual, and included sex, age and the interaction as predictors. For between-season dispersal, we replaced year by period, a variable that represented the lapse between the spring of year  $t$  and the spring of year  $t+1$ .

To assess the factors that may promote or constrain dispersal and divorce, we used GLMMs with a dichotomous response variable (dispersed–not dispersed, or divorce–not divorced) for each individual, and previous nesting success (success or failed), density of territorial males and ASR as predictors. We used the density of territorial males (bachelors + monogamous that actively defend a territory) as a proxy for territory availability, as density and territory availability should be inversely correlated. We estimated the ASR as the ratio between the number of males and females that defended a territory or performed a breeding attempt. Again, individual identity was included in the model as a random factor. We also included mate status (mate alive or absent) for the analysis of between-season dispersal as a further fixed factor. We included those individuals that remained single or lost their partner in the mate absent category (widows or widowers). For single males, we considered their previous nesting success to be zero.

We used a statistical modelling approach (Graven & Hails 2002, Logan 2010) for data analysis. We fitted a full model with explanatory variables and appropriate interaction terms, and then sequentially removed non-significant interaction terms and main effects until only significant terms

remained. We determined the significance of terms using the Wald statistic ( $P < 0.05$ ). We used the `lme4` package (Bates *et al.* 2015) in the R language and environment (R Development Core Team 2013) for all statistical analyses.

### Individual consequences of dispersal and divorce

To evaluate if within- and between-season dispersal and divorce are strategies that increase breeding success, we compared the change in the breeding success (difference in the number of fledglings between consecutive nesting attempts) between individuals that dispersed or divorced and individuals that remained on their territories or retained their mates. We were able to estimate only the apparent breeding success of males, as we did not perform an assessment of extra-pair fertilizations. We performed a GLMM with the change in the number of fledglings produced by individuals that dispersed and did not disperse, or that divorced or did not divorce, as the response variable, and the dispersal/divorce status as a dichotomous predictor. We included the individual identity and year as random factors. For these analyses we assumed a normal error distribution, and an identity link function. As before, we fitted a full model with explanatory variables and appropriate interaction terms, and then sequentially removed non-significant interaction terms and main effects until only significant terms remained. We report significant ( $P < 0.05$ ) results in the text, and full model details are provided as supporting information in the online version of this article. All means are presented  $\pm 1$  se.

## RESULTS

The mean adult breeding population density was  $9.19 (\pm 0.79)$  individuals/ha, but it varied widely during the period studied (range = 5.75–12.25 individuals/ha,  $n = 9$ ). Accordingly, the number of territories varied between years (mean =  $43 \pm 4.1$ , range = 26–62,  $n = 9$ ; Fig. 2a). The mean territory size was  $709.51 \pm 40.85$  m<sup>2</sup> ( $n = 80$ ). The ASR was male-skewed every year (mean ratio = 1.43 males per female, range = 1.02–1.93,  $n = 9$ ; Fig. 2a). We did not observe any ringed adults in neighbouring study forest patches located approximately < 1 and 5 km from our study site during 2007–2010 and 2003–2009, respectively.

### Breeding dispersal

#### *Within-season dispersal*

In total, we registered 120 second nesting attempts following a successful or unsuccessful first breeding attempt within a breeding season. About 30% of breeding individuals dispersed (61/202 ringed individuals). Dispersal probability varied significantly between sexes (Supporting Information Table S1, Fig. 2b). Females dispersed more frequently than males (overall rate: 36.7 vs. 21.6%). No effect of adult age was detected on the probability of dispersal. Most frequently, dispersal involved the movement of an individual or a pair to neighbouring territories (mean dispersal distance =  $47.39 \pm 5.11$  m, range = 15.48–214.68 m,  $n = 61$ ).

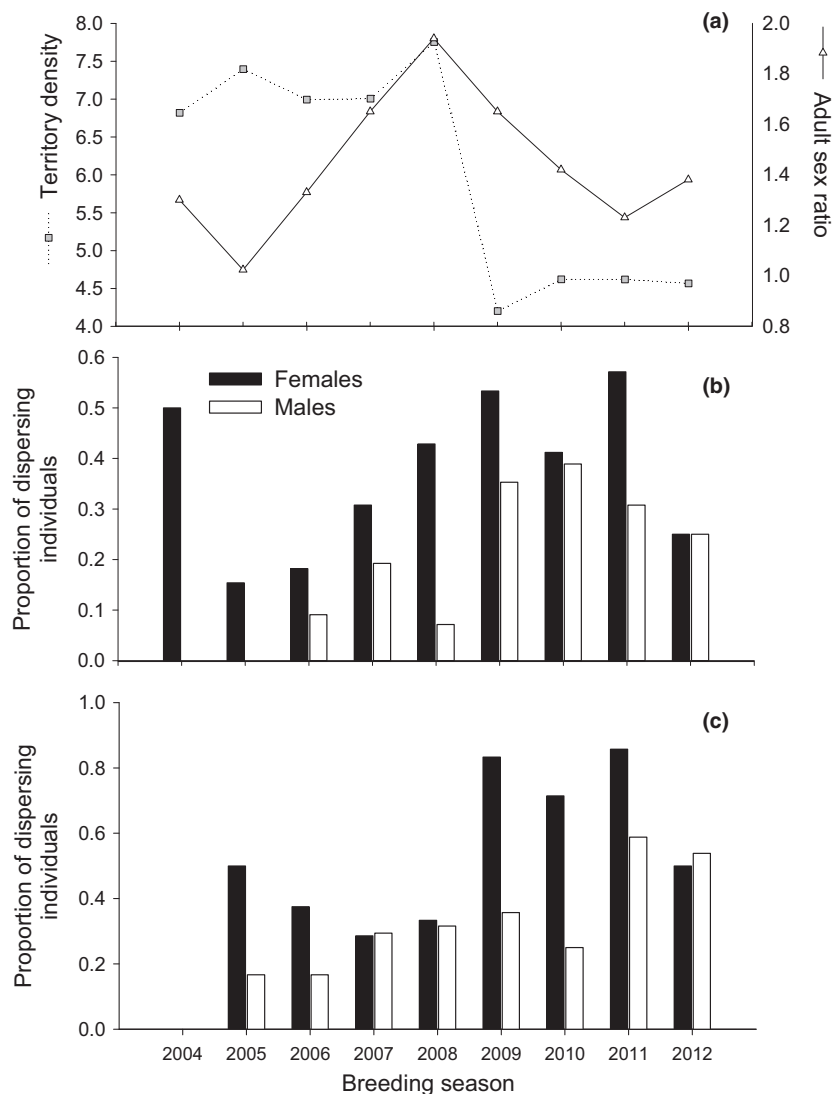
Both male and female dispersal probabilities were affected by territory availability (Supporting Information Table S2, Fig. 3a). Dispersal increased when territory density was lower (i.e. with increased territory availability). For males, we also detected an effect of nesting success (Table S2) but, contrary to expectations, successful males dispersed more frequently than males that failed during the nesting attempt. However, this effect was only evident when we excluded territory availability from the model (Table S2).

Within-season dispersal was not affected by previous breeding success, nor did it increase the breeding performance of individuals that dispersed (Supporting Information Table S3). We did not find evidence that breeding dispersal increased breeding success, as there were no significant differences in the change in the number of fledglings between consecutive breeding events both for Wrens that dispersed and for Wrens that remained in their territories (Table 1).

#### *Between-season dispersal*

About 42% of breeding individuals dispersed between seasons (69/162 ringed individuals). Overall, between-season dispersal was more frequent than within-season dispersal for both males and females (Fisher exact tests,  $P = 0.02$  for females and  $P = 0.01$  for males). Females dispersed more frequently than males (Table S1, Fig. 2c). No effect of age of individuals on the probability of dispersing was detected (Table S1). Similarly to within-season dispersal, individuals most frequently dispersed between seasons to neighbouring territories (mean dispersal distance =  $53.86 \pm 4.02$  m, range = 17.31–214.68 m,  $n = 69$ ).





**Figure 2.** (a) Annual variation in territory density (territories/ha) and adult sex ratio in the study area. (b) Proportion of individuals that dispersed between nesting attempts in the same breeding season (within-season dispersal). (c) Proportion of individuals that dispersed between breeding seasons (between-season dispersal). Black bars: females; white bars: males.

Female dispersal probability was affected mainly by territory density (Table S2). The probability of female dispersal increased when territory density declined (i.e. when territory availability increased; Fig. 3b). Similarly, male dispersal was affected by territory density, but we also detected a significant effect of the interaction between mating status and ASR (Table S2). The interaction suggested that males whose partners remained alive tended to disperse less frequently than single or widowed males when the ASR was more male-biased (Fig. 4).

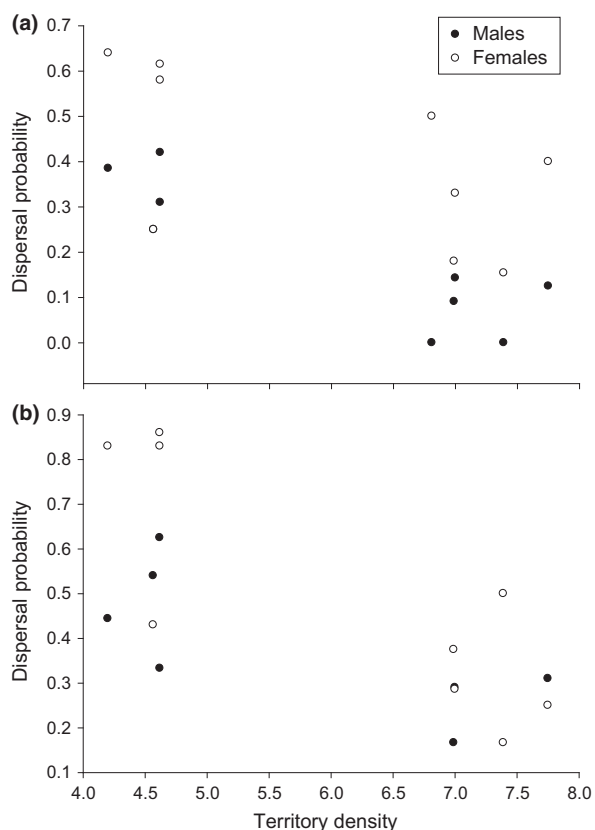
Between-season dispersal was not affected by previous breeding success, nor did it increase the

breeding performance of individuals that dispersed (Table S3). Males and females that dispersed between seasons produced a similar number of fledglings after and before dispersing than non-dispersing individuals (Table 1).

## Divorce

### *Within-season divorce rates*

Overall, 23.3% (28/120) of breeding pairs divorced between nesting attempts within a breeding season (mean =  $23 \pm 4.3\%$ ; range = 0–43%,  $n = 9$ ). Most of the divorce events were initiated



**Figure 3.** Effect of territory density (territories/ha) on the probability of dispersal in Southern House Wrens within (a) and between (b) breeding seasons. Territory availability affected male and female within-season dispersal (Wald  $F_{1,79.8} = 5.79$ ,  $P = 0.018$  and Wald  $F_{1,75.5} = 5.90$ ,  $P = 0.017$ , respectively) as well as between-season dispersal of individuals (males: Wald  $F_{1,95.3} = 7.68$ ,  $P = 0.007$ ; females: Wald  $F_{1,55.0} = 9.75$ ,  $P = 0.003$ ).

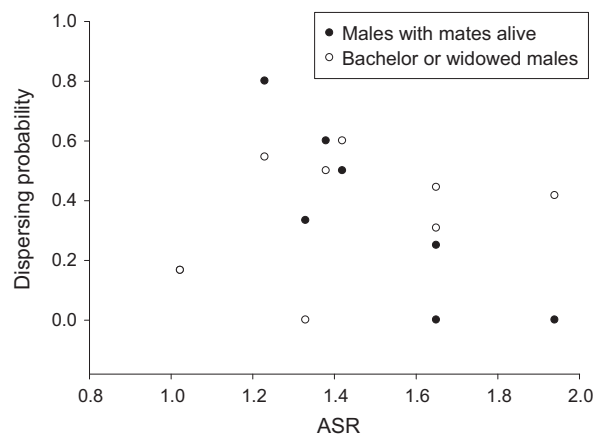
by females; 54.6% of 44 females that dispersed within a breeding season bred with a new partner (initiated divorce), whereas 43.2% remained together with their partners (in one case we did not know the fate of the male). In contrast, 3.9% of the 26 males that dispersed within a breeding season divorced, leaving their mate in the former territory (probably displaced by an intruding male), whereas in 11.5% of the pairs, both adults left the territory and it was not possible to determine which sex initiated the divorce. From the remaining male dispersal events, males dispersed together with their mates in 73% of cases (in three male dispersal events we do not know the fate of females between nesting attempts).

Pairs divorced within a breeding season more frequently when ASR in the population was more

**Table 1.** Change in the number of fledglings produced between consecutive nesting attempts of dispersing/non-dispersing and divorced/non-divorced individuals.

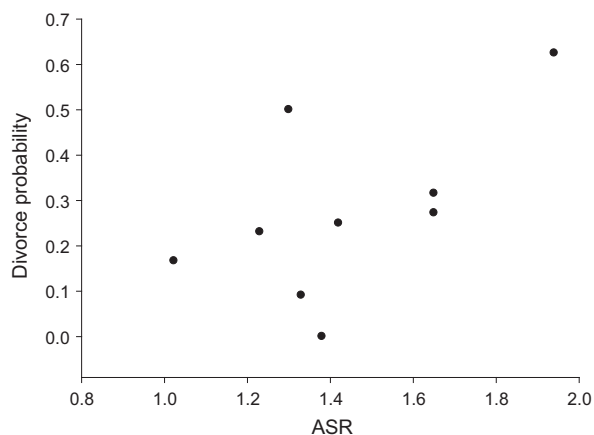
Dispersal	Dispersing individuals	Non-dispersing individuals
Within-season		
Males	0.50 (0.66)	-0.41 (0.35)
Females	0.56 (0.46)	0.26 (0.38)
Between-season		
Males	0.00 (0.69)	0.11 (0.54)
Females	0.71 (0.70)	-0.52 (0.75)
Divorce	Divorced individuals	Non-divorced individuals
Within-season		
Males	-2.25 (0.78)	0.54 (0.38)*
Females	2.25 (0.99)	-0.63 (0.64)*
Between-season		
Males	1.50 (1.53)	-0.93 (1.54)
Females	1.20 (2.19)	0.80 (1.73)

Means ( $\pm$ se) are presented and asterisks indicate statistically significant differences.



**Figure 4.** Variation in dispersal probability in Southern House Wren males in relation to adult population sex ratio (ASR) according to their mating status. An increment in ASR reduced the between-season dispersal probability of paired males, whereas variation in ASR did not affect dispersal of bachelor or widowed males (ASR Mating status effect: Wald  $F_{1,80.1} = 4.70$ ,  $P = 0.033$ ).

skewed towards males (Supporting Information Table S4, Fig. 5). Territory density and previous nesting success did not affect the probability of divorce (Table S4). Divorce appeared to affect the breeding success of individuals (Supporting Information Table S5). After a divorce event, males fledged fewer nestlings, but females increased their reproductive success (Table 1).



**Figure 5.** Variation in the probability of within-season divorce in Southern House Wren breeding pairs according to the adult sex ratio (ASR) in the population. Divorce probability increased with increasing ASR (Wald  $F_{1,94.0} = 5.16$ ,  $P = 0.025$ ).

#### *Between-season divorce rates*

Overall, 35.1% (13/37) of breeding pairs divorced between breeding seasons (mean =  $37.9 \pm 7.4\%$ , range = 20–75%,  $n = 8$ ). We did not detect significant differences in divorce rates between and within breeding seasons (Fisher exact test,  $P = 0.11$ ). Similarly to within-season divorce, most divorce events between breeding seasons were initiated by females. Of 19 dispersing females, 63.2% divorced and 36.8% bred with the same male as in the previous year. Also, 7.1% of 14 males that dispersed divorced, leaving their social partner in the former territory, and 42.9% divorced when both adults abandoned the territory. From the remaining male dispersal events, 50% of males dispersed together with their mates.

We failed to find any effect of adult population density, ASR, previous nesting success or total number of fledglings produced in the previous breeding season on the probability of divorce (Table S4). Furthermore, divorce appears not to affect the reproductive performance of individuals (Table S5). Divorced females and males did not increase the number of fledglings produced significantly compared with non-divorced individuals (Table 1).

## DISCUSSION

Within- and between-breeding season dispersal of Southern House Wrens at our study was moderate (30 and 42%, respectively), with females dispersing more frequently than males. Similarly, within-

and between-season divorce rates were moderate (23.3 and 35.1%, respectively), with females initiating divorce more frequently than males. While dispersal decisions were affected mainly by territory availability, divorce decisions were mainly affected by mating opportunities. Divorce and dispersal were not affected by previous breeding success; however, females increased their breeding success after a divorce event. These results highlight the importance of social and environmental contexts in the dispersal behaviour and stability of social pair bonds.

## Dispersal

In common with our results, higher male site fidelity has been reported in several passerines (e.g. Greenwood 1980, Greenwood & Harvey 1982, Clarke *et al.* 1997, Andreu & Barba 2006, Eeva *et al.* 2008, Valcu & Kempenaers 2008, García-Navas & Sanz 2011), including migratory populations of Northern House Wren (Kendeigh 1941, Drilling & Thompson 1988). Drilling and Thompson (1988) suggested that higher male site fidelity in migratory Northern House Wrens may be a consequence of greater costs of finding a new territory than of re-establishing the territory of the previous year (Greenwood's hypothesis; Greenwood 1980, 1984). However, this hypothesis cannot explain male philopatry in Southern House Wrens, as year-round residency allows the detection of vacant territories during the non-breeding season, reducing the costs of searching for a new territory.

Sex differences in dispersal behaviour in House Wrens may be explained by differences in survival probabilities between sexes. In Northern and Southern House Wrens, males have been reported to have higher adult survival than females (Llambías *et al.* 2015), creating more opportunities for female dispersal in both resident and migratory populations. Accordingly, at our South Temperate site, ASR was always male-skewed, and variation in ASR did not affect female dispersal probability. In contrast, bachelor and widowed males moved more frequently between seasons compared with paired males when population ASR decreased.

In Tropical House Wrens, Freed (1987) proposed that dispersal is constrained by the low availability of vacant territories. A similar constraint may be operating at our South Temperate site, as both between- and within-season dispersal decreased for both sexes when territory availability



decreased. Furthermore, differences in territory availability may also explain the higher between-season dispersal probabilities observed, as increased adult mortality during the austral winter creates greater territory instability between breeding seasons. This pattern suggests that dispersal decisions in the Southern House Wrens may be associated with opportunities to switch to higher quality territories and/or mates (Greenwood 1980, 1984, Otter & Ratcliffe 1996).

Most within- and between-season dispersal events involved short-distance movements to neighbouring territories. Our dispersal estimates could have underestimated true dispersal if we failed to re-sight ringed individuals in neighbouring forests. However, long-distance dispersal seems to be rather infrequent, as House Wren populations in the area are genetically structured, with significant genetic differences between populations that are 5 km distant from each other (Carro 2012).

### Mate switching

Divorce rates for temperate Southern House Wrens were intermediate between those reported for Northern House Wrens (between-season = 57.1–96.3%, Drilling & Thompson 1988, Poirier *et al.* 2003; within-season = 35.2–58.0%, Drilling & Thompson 1991, Poirier *et al.* 2003) and Tropical House Wrens (between-season = 1% and within-season = 2%, Freed 1987). At our study site, 50% of individuals that dispersed moved together as a social unit, suggesting a strong pair bond between socially monogamous pairs. Opportunities for divorce and re-mating may explain the observed differences in the House Wren complex. In Northern House Wrens, males may desert the brood or reduce parental care to attract additional mates, increasing opportunities for divorce (Drilling & Thompson 1991). In a similar way, females may desert the brood late in the nestling period to start a second brood with a different mate (Drilling & Thompson 1991). In contrast, in Tropical House Wrens, habitat saturation may reduce mate availability, constraining the divorce rates (Freed 1987). We observed a similar constraint on within-season divorce in our South Temperate population, as suggested by the positive relationship between divorce rate and the population ASR. An increased male to female ratio probably favours mate switching, as it increases the opportunities for females to locate new

partners. Also, the low adult survival rates reported for Northern, Tropical and Southern House Wrens (e.g. Freed 1986, Drilling & Thompson 1991, Young 1994, Llambías *et al.* 2015), coupled with variation in recruitment rates, may be responsible for the high variation in territory occupancy along the species' range, and therefore the opportunities for divorce and/or dispersal. However, the relationship between divorce rates, resident lifestyle, adult survival and mating opportunities in the House Wren complex proves not to be a simple one and deserves further evaluation.

### Benefits of breeding dispersal and divorce

The advantages of breeding dispersal and divorce remain elusive in the House Wren complex. In both Tropical and North Temperate House Wrens, divorce and mate retention were not associated with breeding performance, nor are these strategies to increase breeding success (Freed 1987, Drilling & Thompson 1991). Similarly, in our South Temperate population, Southern House Wren dispersal and divorce were not related to previous breeding performance. However, after a within-season divorce, female breeding success increased, whereas male breeding success decreased. Hence, males seem to pay a cost for divorce, in some cases because they were unable to find a new mate.

Our failure to find other benefits from dispersal/divorce in the Southern House Wren does not imply that dispersal or divorce are not adaptive strategies, as indirect benefits were not evaluated (e.g. endogamy avoidance, individual phenotypic quality variation or reduction of kin competition; Greenwood 1980, 1984). Furthermore, it has been suggested that dispersal decisions could be based on more than one factor (Greenwood & Harvey 1982, Cézilly *et al.* 2000, Beheler *et al.* 2003), and that their relative importance could vary according to the environmental and social contexts in which individuals find themselves (Drilling & Thompson 1991).

### CONCLUSIONS

Our results suggest that dispersal and divorce decisions in the Southern House Wren are affected by the environmental and social contexts in which individuals find themselves. However, these

decisions may vary according to the opportunities and interests of each of the sexes. In our population, a strong ASR skew towards males may constrain male dispersal and divorce decisions. In contrast, this same social context may provide females with greater opportunities for dispersal and divorce. Besides these differences, divorce rates and dispersal remain moderate in our temperate Southern House Wren population, showing a relatively high territorial and mate fidelity. Temporal variation in territory availability and ASR seems to affect dispersal and divorce rates, suggesting a dynamic character to the dispersal behaviour of this species.

We thank Luis García for allowing us to work on his ranch in Buenos Aires, and Martha Busai, Mario Beade and families for logistical support. We also thank C. Battagliese for her assistance with English grammar, Dan Chamberlain for useful comments and suggestions and two anonymous reviewers who revised an earlier version of the manuscript. This work was supported by the University of Buenos Aires (UBACyT 20020090200117) and CONICET (PIP112-200901-00011) grants to G.J.F. Financial support for P.E.L. was provided by CONICET (PIP 11220130100198 and D1791) and FONCYT (PICT 2010-1033). All methods used in the present study meet the ethical requirements for science research and comply with the current laws of the country in which they were performed.

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Received 28 September 2015;  
revision accepted 26 October 2016.  
Associate Editor: Luc Lens.

## SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

**Table S1.** Summary of the results for the analysis of the variation according to sex, age of individuals and year of the probability of dispersal of breeding Southern House Wrens.

**Table S2.** Summary of the effects of previous nesting success, adult sex ratio (ASR), and territory density on the probability of dispersal of male and female Southern House Wren individuals within and between breeding seasons. We only present simple effects and interaction effects with  $P < 0.1$ .

**Table S3.** Reproductive consequences of breeding dispersal within and between breeding seasons for male and female Southern House Wrens.

**Table S4.** Summary of the effects of previous nesting success, adult sex ratio and territory density on the probability of divorce of Southern House Wren mating pairs within and between breeding seasons. Past productivity represents the total number of fledglings produced in the previous breeding season.

**Table S5.** Reproductive consequences of divorce within and between breeding seasons for male and female Southern House Wrens.