

1 Running head: Nest and mate choice in white-rumped swallows

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3 **Sexual differences in the effect of previous breeding performance on nest-box reuse**
4 **and mate retention in white-rumped swallows (*Tachycineta leucorrhoa*)**

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21

22 **Abstract**

23 In birds, the selection of nesting sites and mates has a profound influence on the daily
24 interactions of individuals. Both behaviours are energetically costly and time-
25 consuming and can strongly affect Darwinian fitness of individuals. Using a 12-yr
26 dataset on banded returning breeders, we explored variables associated with nest-box
27 choice and mate choice in the White-rumped Swallow, a socially monogamous
28 migratory passerine. Females reusing nest-boxes, but not males, produced significantly
29 more fledglings than did those that changed nest-boxes. Females and males that retained
30 mates produced significantly more fledglings than did those that divorced. General
31 linear mixed models revealed that the number of fledglings produced in previous
32 seasons significantly explained the reuse of particular nest-boxes by females, but not by
33 males. Mate choice by females was not strongly affected by either past breeding
34 performance or nest-box reuse, but nest-box reuse alone predicted mate choice by
35 males. Nest-box reuse by males was apparently more related to retention of female
36 partners. This study revealed that sexual differences in the nesting and mating decisions
37 were guided by the use of information on past breeding performance in a subtropical,
38 secondary cavity nester.

39

40 **Additional keywords:** cavity nester, mating behaviour, migratory, Neotropical, nesting
41 site fidelity.

42 **Introduction**

43 Nest-site selection and mate choice, two fundamental aspects of the breeding behaviour
44 of birds, have intrigued researchers ever since Darwin (Darwin 1871; Danchin and
45 Cézilly 2008). Such behaviours vary widely both within and among species, have been
46 extensively investigated and experimentally tested (e.g., Lindén 1991; Ens *et al.* 1993;
47 Haas 1998; Bai and Severinghaus 2012) and continue to be actively explored (e.g., Lv
48 *et al.* 2016). Because both activities affect daily interactions between organisms and are
49 energetically costly and time-consuming, nest-site selection and mate choice have
50 important consequences for individual fitness and are under strong selection pressure
51 (Boulinier *et al.* 2008; Kivelä *et al.* 2014).

52 In natural populations of socially monogamous passerines, nest-site selection is affected
53 by many variables. A prior successful reproductive experience has long been considered
54 a major influence on returning to certain breeding grounds (Greenwood and Harvey
55 1982, Winkler *et al.* 2004) and on nest fidelity (García-Navas and Sanz 2011).
56 Moreover, nest-site selection can vary according to sex, age, reproductive experience,
57 previous breeding performance, seniority in nest-use, time of arrival at the breeding
58 grounds (Choudhury 1995; Hoover 2003; Llambías *et al.* 2008), and intrasexual
59 competition (Bai and Severinghaus 2012), among other factors. Quality of the nest-site
60 also affects selection. Whether nest quality can be predicted from one breeding season
61 to another remains uncertain (Wischhoff *et al.* 2015), although assessment of nest
62 quality and subsequent fidelity to the preferred nest is fairly common in passerines
63 (Greenwood 1980; García-Navas and Sanz 2011; Hussell 2012; Robillard *et al.* 2013).
64 Thus, nest-site selection is also affected by the spatial location, size, shape and
65 protection from predators (Rendell and Robertson 1989; Lambrechts *et al.* 2010), in
66 addition to the internal temperature and cardinal orientation (Ardia *et al.* 2006).

67 Similarly, mate choice is linked to factors that are indicative of mate quality, such as
68 breeding experience (Lv *et al.* 2016), age (Edme *et al.* 2016), genetic components (Arct
69 *et al.* 2015), external morphological traits (e.g., plumage colouration, ornamentation;
70 Whittingham and Dunn 2016), and physical condition (Guindre-Parker *et al.* 2013). In
71 seasonally monogamous species with biparental care, breeding performance partly relies
72 on the breeding ability of a mate, which implies that reuniting with a high-quality
73 partner will improve individual lifetime fitness (Stutchbury and Morton 2008). If mate
74 choice is influenced by the quality of a mate, then mate fidelity will occur when the

75 reproductive success with the same partner is above the average value expected for
76 other candidates (Choudhury 1995). Thus, breeders that are successful are expected to
77 remain together for the long term (Hoover 2003; Gill and Stutchbury 2006; Bai and
78 Severinghaus 2012). This mate fidelity accommodates a ‘win-stay, lose-switch’ model
79 (Switzer 1993) in which individuals show fidelity after a good reproductive
80 performance (Bai and Severinghaus 2012; Campomizzi *et al.* 2012). In this way, birds
81 make use of *a priori* information on their own breeding experiences to predict future
82 outcomes (Boulinier *et al.* 2008).

83 Nest selection and mate choice often interact in a complex manner with the result that
84 either can be a by-product of the other (Choudhury 1995; Bai and Severinghaus 2012;
85 Lv *et al.* 2016). Two examples of this interaction are the following: i) divorce due to the
86 dispersal of a pair member from a particular breeding site after experiencing
87 reproductive failure (Choudhury 1995) and ii) nest-box claiming, which serves as a cue
88 of increased competitive ability and good reproductive performance for potential
89 partners (Fokkema *et al.* 2016).

90 Most studies on nest-site selection and mate choice in passerines have been conducted
91 with north-temperate species (Stutchbury and Morton 2008); whereas information on
92 Neotropical species is limited (Gill and Stutchbury 2006; Aguilar and Marini 2007;
93 Wischhoff *et al.* 2015). Among north-temperate species, the Tree Swallow *Tachycineta*
94 *bicolor* uses its own breeding experience to choose among breeding colonies and nest-
95 boxes and to make decisions about philopatry and mate fidelity (Llambías *et al.* 2008;
96 Lessard *et al.* 2014). In this study, we focused on the subtropical White-rumped
97 Swallow (*Tachycineta leucorrhoa*) (Aves, Passeriformes: Hirundinidae; hereafter
98 denoted collectively as WRS). This species is an obligate secondary cavity nester
99 (Turner and Rose 1989), which readily occupies artificial nest-boxes and shows
100 philopatry to breeding grounds (Bulit and Massoni 2011). Similar to other aerial
101 insectivores, WRS individuals do not defend foraging territories, but early in the
102 breeding season, they compete for nesting sites and fiercely defend their chosen nest-
103 boxes and immediate surroundings against intruders, including conspecifics (Fig. S1,
104 this work; Massoni *et al.* 2007). Although WRS individuals are socially monogamous,
105 they show high rates of extra-pair paternity (EPP) (up to 77 % of broods at our study
106 site, Ferretti *et al.* 2011). The species exhibits biparental care, but females make
107 approximately 60 % more feeding visits *per* nestling *per* hour than males and remove

108 30-40 % more faecal sacs when nestlings are 12-15 d old (Bulit *et al.* 2008). Similar to
109 other migrants, to increase the probability of achieving a successful reproductive cycle,
110 each season these birds must make mating decisions in a short time frame (Choudhury
111 1995; Ferretti and Winkler 2009). Based on these decisions, this seasonally
112 monogamous species can suffer high fitness costs, mostly derived from constraints
113 related to the search for new nesting sites and mates.

114 Here, we used a 12-yr dataset on returning breeders to test the hypothesis that sexes
115 would differ in the way different variables influenced nest-box and mate choice
116 behaviours in WRS. In most migratory birds (Kokko *et al.* 2006), including tree
117 swallows (Robertson *et al.* 1992; Lozano 1994), males arrive earlier than females at the
118 breeding grounds. Additionally, in many species, including tree swallows (Robertson *et al.*
119 *et al.* 1992), males and females play different roles in nest-box acquisition and defence
120 and in mate choice. Previous evidence for WRS suggests that females actively return to
121 a breeding site after successful reproductive experiences (Bulit and Massoni 2011) and
122 make a significantly larger parental investment than males (Bulit *et al.* 2008). For tree
123 swallows, the evidence suggests that they use self-information on previous breeding
124 experience to select nest-sites (Llambías *et al.* 2008; Lessard *et al.* 2014). Taking this
125 into account and assuming that WRS behave similarly to their congeners, in the context
126 of a ‘win-stay, lose-switch’ model (Switzer 1993), we expect that 1) previous breeding
127 experience will affect nest-box reuse by females. Additionally, given that female WRS
128 increase their fitness via extra-pair copulations (Ferretti *et al.* 2011), we expect that 2)
129 mate retention will have less influence on nest-box reuse by females. Conversely, given
130 that males can greatly increase their fitness by siring offspring in several nests (EPP,
131 Ferretti *et al.* 2011), we expect that 3) previous breeding experience will have a minor
132 influence on nest-box reuse by males. Each season, female WRS seek a mate with good
133 parental abilities to raise a successful brood; therefore, we expect that 4) previous
134 breeding experience will influence mate retention by females. Additionally, if males
135 attract attention from females through nest-box defence (as cue of good parental
136 abilities, Burtka and Grindstaff 2015), we expect that 5) nest-box choice will greatly
137 influence mate retention by males.

138

139 **Methods**

140 *Study species, study system and data collection*

141 White-rumped swallows are small passerines (*ca.* 22 g) that breed from Buenos Aires
142 Province (Argentina) to northern Bolivia and southern Brazil (Turner and Rose 1989).
143 WRS are primarily single-brooded, with an average clutch size of five eggs and an
144 average brood size of four nestlings (Massoni *et al.* 2007; Ferretti *et al.* 2011). Data for
145 this study were collected during the breeding seasons of 2002-2015 at a site located in
146 an agricultural landscape in Chascomús, Argentina (35°34'S, 58°01'W), in which a
147 system of nest-boxes has been in use since 2002. Nest-boxes measured 25 × 17 × 13
148 cm, had an entrance hole 4 cm in diameter, a lateral door to monitor the nest's progress,
149 and a 'wigwag' trap to capture the breeding adults when they entered the box (Massoni
150 *et al.* 2007). All nest-boxes were equivalent in relevant physical features, were made of
151 the same wood (pine) and quality, and had identical shapes and sizes. Nest-boxes were
152 separated by *ca.* 30 m, distributed over *ca.* 63 ha, mounted on metal poles between 1.3
153 and 1.7 m above the ground and attached to the primary fence posts around cattle
154 enclosures and cultivated or pasture fields of various sizes, shapes and locations (see
155 Massoni *et al.* 2007 for further details).

156 During the study period, each nest-box had a precise and constant geographical location
157 (i.e., primary fence posts were never moved), but the orientation of the entrance holes of
158 nest-boxes varied many times throughout the study period to accommodate farm
159 management. Nest-boxes were located either in the open pampas or more protected
160 areas (e.g., near tree plantations, buildings or granaries) and exposed to different
161 microclimatic conditions. We believe that the orientation of entrance holes was not a
162 significant factor, at least in this location. Therefore, all nest-boxes were considered to
163 be of equal value as a resource. Nest-boxes were geo-referenced with a Garmin 76 GPS
164 to the nearest 3 m and uniquely identified with numbers or letters. At the onset of each
165 breeding season, we removed old nest material from the nest-boxes before swallows
166 arrived. The number of boxes available for nesting varied among years (Fig. S2).

167 The breeding season of WRS at our study site lasts approximately 3.5 months, from
168 October to mid-December (Massoni *et al.* 2007), but individuals arrive and start
169 claiming nest-boxes in early/mid-August. We checked nest-boxes daily from the
170 beginning of nest lining to detect the onset and progression of the egg-laying sequence.
171 During incubation, we visited nests every two days until one day before the presumed
172 date of egg hatch after which we resumed the daily visits. Development was recorded
173 every two days until nestlings were 12 days old, when we stopped visits to avoid

174 causing premature fledging; one day after the expected departure date we returned to the
175 nest to record the number of nestlings that fledged successfully. Adults were captured
176 inside the nest-box using a ‘wigwag’ trap, which consists of a swivelling piece of wood
177 that is activated when the focal bird enters the box by pulling a long piece of fishing line
178 attached to the trap (further details in Massoni *et al.* 2007).

179 Females were captured during incubation, and males were captured while feeding
180 nestlings (as in Massoni *et al.* 2007). Adults and 8-d-old nestlings were banded with a
181 uniquely numbered aluminium ring. For each captured adult, we recorded band number,
182 identity of the box in which it was captured, sex (determined by the presence of a brood
183 patch or cloacal protuberance), mate identity (if known), and number of fledglings
184 produced. Because WRS adults show no age-related external morphological characters,
185 only those that had been banded at the Chascomús colony as nestlings (i.e., recruits)
186 could be accurately aged. WRS adults captured for the first time were considered to be
187 at least 1-yr-old, assuming that they were born in the previous year at a different
188 location and taking into account that natal dispersal is more extensive than breeding
189 dispersal in this species (Bulit and Massoni 2011).

190 Data collection and biological sampling were conducted in compliance with the
191 guidelines for the care and manipulation of animals established by the Facultad de
192 Ciencias Exactas y Naturales de la Universidad de Buenos Aires (Argentina) and under
193 permits from Dirección de Flora y Fauna del Ministerio de Asuntos Agrarios de la
194 Provincia de Buenos Aires (Argentina) (permission no. 65/07).

195 ***Data analyses and statistical methods***

196 We computed rates of returning breeders, rates and patterns of nest-box occupancy and
197 patterns of mate choice (see below). We focused on variables associated with nest-box
198 and mate choice made by returning birds in subsequent breeding seasons (either
199 consecutive or not), which are defined in Table 1. We compared the number of
200 fledglings produced by birds in relation to their choices of nest-boxes or mates using
201 *Tukey-Kramer* tests, corrected for small and unequal sample sizes.

202 We first investigated the possible effects of age on the previous breeding performance of
203 WRS, as reported for tree swallows (Robertson and Rendell 2001) and fitted general
204 additive mixed models (GAMMs) (Wood 2000), as in Zhang *et al.* (2015). GAMMs
205 include linear predictors involving a sum of smooth functions of covariates, which

206 allow for a flexible specification of the dependence of the response (Wood 2006). We
207 modelled age as a fixed predictor of the number of fledglings produced (response
208 variable, Poisson distribution, log link function, setting it as a penalised thin-plate
209 regression spline (smooth function)), with a K of 6, and the degree of smoothness was
210 determined by cross-validation (Wood 2003, 2004). Within the fixed predictors, we also
211 set nest-box choice (categorical variable with two levels: ‘reuse’ or ‘change’; Table 1)
212 and mate choice (categorical variable with two levels: ‘retention’ or ‘divorce’; Table 1).
213 To account for pseudoreplication, individual identity (band number) nested within
214 calendar year was set as a random effect; to account for variation in the number of
215 boxes available during the study period, calendar year was also set as an additional
216 random effect (as in Béziers *et al.* 2016).

217 To explore predictors of nest-box choice, we fitted different sets of general linear mixed
218 models (GLMMs) (Breslow and Clayton 1993; Bolker *et al.* 2009; Crawley 2012) using
219 a larger dataset (n : females = 241, males = 104), in addition to a trimmed dataset (n :
220 females = 92, males = 96), of observations with associated information on mate choice.
221 Nest-box choice was set as the response variable (binomial error distribution, logit link
222 function) with the number of fledglings produced in the previous season as a fixed
223 predictor (larger dataset) or this variable and mate choice as fixed predictors (trimmed
224 dataset). In models with mate choice as the response variable (binomial error
225 distribution, logit link function; trimmed dataset only), the number of fledglings
226 produced in the previous season and nest-box choice were set as fixed predictors.
227 Random effects in GLMMs were the same as described above for GAMMs.

228 All analyses were performed in the R v.3.3.0 statistical software package (R
229 Development Core Team, 2016) using the mgcv package v.1.8–12 (Wood 2016) for
230 GAMMs and the lme4 package v.1.1-12 (Bates *et al.* 2013) for GLMMs. We fitted all
231 models derived from the combination of all fixed predictors plus all the interactions
232 among them and also tested the null model (without fixed effects). Initial exploratory
233 modelling using a pooled dataset of females and males revealed that sex was a
234 significant fixed predictor; therefore, final analyses were conducted separately for the
235 sexes. Model selection followed the information-theoretic approach (Burnham and
236 Anderson 2002), based on the Akaike Information Criterion (AIC). The model with the
237 lowest AIC was considered the best-fitting model. Effect sizes were examined by
238 standardising estimates using ‘partial.sd’ (Cade *et al.* 2015) and by computing 95 %

239 confidence intervals (CI) around estimates; CI excluding zero were considered
240 significant (as in Pellerin *et al.* 2016).

241

242 **Results**

243 ***Rates of returning breeders, nest-box occupancy and mate choice***

244 Between 2002 and 2015, we banded 3,081 white-rumped swallows; of these, *ca.* 20 %
245 were adults (399 females, 217 males) and 2,465 were nestlings, resulting in an average
246 local recruitment rate of 4.2 % (41 females, 62 males). The average returning rate of
247 adults was 29.7 % and no significant differences were found between sexes (returning
248 females: 31.8 %, $n = 127$; returning males: 25.8 %, $n = 56$; odds ratio = 0.060, $P =$
249 0.14). Most females and males returned to the colony twice; females and males
250 returned for up to six and five seasons, respectively. Among returning adults, 26 % of
251 the females and 22 % of the males had failed to breed in at least one previous season at
252 the study site. The primary causes of nest failure were predation by snakes, rodents or
253 ants (20 % to 50 %), egg loss during competition for nest-boxes with other cavity
254 nesters such as the Southern House Wren (*Troglodytes aedon*), the Saffron Finch
255 (*Sicalis flaveola*) and the House Sparrow (*Passer domesticus*) (10 % to 30 %), and nest
256 abandonment due to cold and rainy weather (12 % to 30 %).

257 Over the study period, on average, 108.4 nest-boxes were available at the Chascomús
258 site, with 60 % occupied by WRS breeders (range: 31.5 % in 2002 to 73 % in 2015, Fig.
259 S2). Reuse of nest-boxes represented 43.5 % and 53.8 % of nest-box choices made by
260 females and males, respectively (total no. observations: reuse $n = 161$, change $n = 184$;
261 Fig. 1). We failed to detect significant differences in rates of nest-box reuse or change
262 between sexes (Fisher's exact test: -0.10, $P = 0.09$). Seventy-six and 43 different
263 females and males reused nest-boxes, respectively, with the females using up to four
264 and the males using up to five different nest-boxes. Females retained mates in 16.3 % of
265 mating events, and males retained mates in 58.3 % of mating events (no. observations:
266 retention = 36, divorce = 152; Fig. 1). We failed to detect significant differences in rate
267 of mate retention or divorce between sexes (Fisher's exact test: -0.05, $P = 0.36$).

268 Fourteen different females and 20 different males reunited at least once with a
269 previously chosen mate. In approximately one quarter (26 %) of the divorces, the
270 previous mates of females were present in the colony paired with other females, with

271 this value being approximately 35 % for males. Most individuals (32 females, 35 males)
272 that divorced also changed nest-boxes (Fig. 1).

273

274 **Determinants of breeding performance**

275 Females, but not males, reusing nest-boxes produced significantly more fledglings
276 (mean \pm *SD* = 3.69 \pm 0.19) than those that changed nest-boxes (mean \pm *SD* = 3.01 \pm
277 0.17; *Tukey-Kramer* $F = 7.16$, $P = 0.008$). Likewise, females that retained mates
278 produced significantly more fledglings (mean \pm *SD* = 4.0 \pm 0.50) than divorcing
279 females (mean \pm *SD* = 3.69 \pm 0.22; $F = 3.89$, $P = 0.02$); and males that retained mates
280 produced significantly more fledglings (mean \pm *SD* = 3.81 \pm 0.41) than did divorcing
281 males (mean \pm *SD* = 3.55 \pm 0.22; $F = 1.73$, $P = 0.04$).

282 We found no evidence of a significant age effect on the breeding performance of WRS
283 males and females. The GAMM that best fit data on the number of fledglings produced
284 by females included age, nest-box choice and mate choice as fixed predictors (UBRE
285 score = 0.27, AICc = 387.97, 3.58 % of the variation explained). However, only nest-
286 box choice was a significant predictor, and neither age ($\chi^2 = 2.22$, *e.d.f.* = 4) nor mate
287 choice was significant. GAMM results showed that females reusing nest-boxes had a
288 higher probability of producing more fledglings ($E \pm SE$: 1.36 \pm 0.10; 95 % CI 1.22–
289 1.50) than those that changed nests (1.22 \pm 0.10; 95 % CI: 1.00 – 1.41). In males, the
290 model that best fit the data included age and mate choice, but neither of these fixed
291 predictors was significant (UBRE score = 0.41, AICc = 411.63, 7.59 % of the variation
292 explained).

293

294 ***Predictors of nest-box choice and mate choice***

295 Using the larger dataset, we found that the number of fledglings produced in the
296 previous season significantly predicted nest-box choice by females (Table 2a, Fig. 2).
297 The null model better explained variation in nest-box choice by males (Table 2b). Using
298 the trimmed dataset, for females, the better fitting model showed that only the previous
299 season number of fledglings had a significant effect on nest-box choice (Table 2c). In
300 contrast, for males, the better fitting model showed that only divorce significantly
301 explained nest-box choice (Table 2d). When exploring mate choice as the response, the

302 null model better fit the dataset for females (Table 2e), whereas nest-box reuse
303 significantly predicted variation in the mate choice of males (Table 2f, Fig. 2).

304

305 **Discussion**

306 ***Rates of returning breeders, nest-box occupancy and mate choice***

307 The observed rate of returning breeders during the 12-yr study period (29 %) was lower
308 than that reported for WRS in southern Brazil (37 %, two seasons; Wischhoff *et al.*
309 2015). Both sexes returned to breed at the Chascomús site at similar rates; most
310 returning females (74 %) and males (78 %) had produced fledglings in at least one
311 previous season, as occurs in other passerines (Hoover 2003). WRS occupied, on
312 average, 60 % of the nest-boxes available at our study site (Fig. S2), a rate higher than
313 that recorded for the species in Santa Fe, Argentina (42.6 %, three seasons; Lorenzón
314 and Quiroga 2012). The observed occupancy rates fall within the range reported for tree
315 swallows at different nesting sites (13–100 %; Winkler *et al.* 2004; Ghilain and Bélisle
316 2008; Hussell 2012). Several variables affect nest-box occupancy rates in swallows
317 (Hussell 2012; Shutler *et al.* 2012), including interspecific competition (Robillard *et al.*
318 2013) and orientation of entrances of nest-boxes (Ardia *et al.* 2006). Nest-box
319 occupancy by WRS in this study could have been affected by competition with saffron
320 finches, southern house wrens (Massoni *et al.* 2007) and more recently, by house
321 sparrows, which are known to affect tree swallows (Ghillain and Bélisle 2008; Robillard
322 *et al.* 2013).

323 Nest-box reuse was 46.6 % of the decisions made by WRS. Most of the reused nest-
324 boxes fledged nestlings, which is consistent with studies of tree swallows showing that
325 prior breeding success in a given nest-box increases the probability of occupation the
326 following season (Ghilain and Bélisle 2008; Lessard *et al.* 2014). Notably, although
327 unused nest-boxes were available in all breeding seasons, WRS fiercely contested for
328 particular nest-boxes (Fig. S1), which were often the ones they had used in a previous
329 season. If WRS are not attracted by the quality of the nest-box *per se* and defend nest-
330 boxes and surroundings rather than foraging territories, then what are the factors
331 influencing nest-box choice in this species? Ardia *et al.* (2006) found evidence that tree
332 swallows prefer east- and south-facing boxes and that nest-box orientation was
333 correlated with the internal nest temperature. However, because we rotated the entrance
334 orientation of nest-boxes during the study period (see Methods) and did not measure

335 internal temperature of the nests, we could not analyse the effect of nest-box orientation.
336 Nonetheless, WRS returned to and reused nest-boxes irrespective of the changes in their
337 particular orientation. In future studies, the influence of the entrance orientation of
338 boxes on nest choice by WRS requires investigation.

339 Intraspecific divorce rates can vary widely among breeding locations and seasons
340 (Choudhury 1995). The observed rates of divorce in WRS were relatively high (females:
341 74 %, males: 65 %) but comparable with those reported for tree swallows in studies of
342 similar duration (83 % in 12 seasons, Shutler *et al.* 2003; 76 % in 14 seasons, Llambías
343 *et al.* 2008). However, because most of the individuals that divorced also changed nest-
344 boxes, the ability to distinguish these forms of choice was limited.

345

346 ***Predictors of nest-box choice and mate choice***

347 We found evidence supporting an experience-based choice in nest-box use for WRS.
348 Nest-box reuse by a female was apparently influenced by previous reproductive success,
349 consistent with the ‘win-stay, lose-switch’ model (Switzer 1993). Although the best
350 fitting models included previous reproductive experience in both sexes, the effect of this
351 variable differed between sexes (Table 2). As expected, the number of fledglings
352 produced at a given nest-box in a previous season significantly explained its reuse by
353 females, but not by males (Table 2a, b). Our results are consistent with preliminary
354 evidence obtained for WRS from Brazil, which suggests that birds failing to breed or
355 that have smaller broods evaluate new, suitable nest-boxes more frequently and farther
356 from their nests than successful conspecifics ($n = 10$ prospectors, two seasons;
357 Wischhoff *et al.* 2015). Sexual differences in the use of self-information have also been
358 reported for blue tits (*Cyanistes caeruleus*) in which the effect of prior breeding
359 experience on the decision to change nesting sites was less clear in males than in
360 females (García-Navas and Sanz 2007).

361 We also found sexual differences in how mate choice mediated nest-box choice. A poor,
362 past reproductive experience associated with divorce significantly predicted nest-box
363 choice by females (Table 2c), whereas in males, mate retention alone significantly
364 affected nest-box choice (Table 2d). When exploring mate choice, neither past breeding
365 performance nor nest-box reuse had strong effects in females (Table 2e), but nest-box
366 reuse alone predicted mate choice by males (Table 2d). The significant effect of
367 previous breeding performance on nest-box choice suggested that returning WRS

368 females relied on their own breeding experience to choose nest-boxes and reused a nest-
369 box after a successful experience. The lack of any significant effect of breeding
370 performance on mate choice by female WRS is consistent with a study of tree swallows
371 that found that low fledging success may not significantly increase the likelihood of
372 breeding with a new mate (Llambías *et al.* 2008).

373 Pioneer observations in tree swallows indicate that females compete for males that
374 occupy a nest-site and not the nest-site itself (Leffelaar and Robertson 1985). If, similar
375 to their congeners, female WRS prefer nest-boxes already occupied by males, and if
376 those males establish in previously used boxes, then nest-box reuse would mediate mate
377 choice in males, as observed in this study. In most migratory birds (Kokko *et al.* 2006),
378 including tree swallows (Robertson *et al.* 1992; Lozano 1994), males arrive earlier to
379 the breeding grounds than females. Most often, early arriving males are usually good
380 flyers and good foragers and therefore, are in better physical condition (Lozano 1994;
381 Bowlin and Winkler 2004; Llambías *et al.* 2008; Lombardo and Thorpe 2010). Thus,
382 earlier returning males may outcompete later ones for the preferred nest-boxes; WRS
383 may also follow this pattern, with early arriving males choosing among available nest-
384 boxes and then fighting and succeeding in occupying the preferred ones. Based on field
385 observations, WRS engaged in violent contests near nest-boxes (Fig. S1). In tree
386 swallows, male nest-box selection influences female mate choice (Lessard *et al.* 2014),
387 which could also apply to WRS in which males provide significant offspring care (Bulit
388 *et al.* 2008) and guard the area around the nest-box during incubation (Bulit and
389 Massoni 2011). Therefore, female WRS would benefit from choosing males in good
390 physical condition because those males could also be good caregivers. Considering all
391 of the above, we suggest that males that occupied the same nest-box as the previous
392 year were of better quality than those that did not and by attracting the attention of
393 females, signalled their condition by claiming and fighting for the nest-boxes. Females
394 WRS may indirectly assess male qualities by choosing those settled in the preferred
395 nest-boxes; such ‘high-quality’ males would supply enough food and parental care to
396 chicks. Additionally, females paired to ‘high-quality’ males would have further
397 opportunities to increase their reproductive success by breeding earlier in the season
398 (Bowling and Winkler 2004; Massoni *et al.* 2007; Liljeström *et al.* 2012). However, to
399 more fully understand the correlates of mate choice in WRS, further studies should
400 investigate the links among food availability, foraging performance and parental skills.

401 Sexual differences in nest-box and mate choice can also be affected by variables other
402 than those explored in this study, such as intraspecific brood parasitism (tree swallows,
403 Whittingham and Dunn 2001), egg dumping [violet-green swallow (*Tachycineta*
404 *thalassina*); Kleiber *et al.* 2007], and extra-pair fertilisation (EPF) (Ferretti *et al.* 2011).
405 We found no evidence of the first two in WRS, although brood parasitism could have
406 remained unnoticed if it occurred the day after resident females had completed egg-
407 laying. Although extra-pair paternity analyses were beyond the scope of this study, up to
408 77 % of broods contained EP offspring at our study site (Ferretti *et al.* 2011). This high
409 prevalence of EPF suggested that extra-pair copulation behaviour was unlikely to affect
410 choice of a nest-box or a social mate.

411 Based on the combined results, our study revealed sexual differences in the effects of
412 own breeding experience on mating decisions by WRS. To reuse a nest-box, females
413 relied more on their previous breeding experiences, whereas in males, nest-box reuse
414 was more related to retaining partners. This study contributed novel insights into the
415 correlates of mating decisions in white-rumped swallows and added to the growing
416 body of evidence that nest site selection in migratory passerines might be mediated by
417 the use of information on past own reproductive experience.

418

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615

FIGURE CAPTIONS

616 **Figure 1.** Number of fledglings produced by female and male white-rumped swallows
617 breeding at the Chascomús site, Argentina, between 2003 and 2015 in relation to age, nest-
618 box choice (change or reuse) and mate choice (retention or divorce).

619 **Figure 2.** Schematic representation of the summary results from GLMMs that explored
620 variables associated with nest-box choice and mate choice in female (a) and male (b) white-
621 rumped swallows returning to breed at the Chascomús site (Argentina) between 2003 and
622 2015. Previous breeding performance was a significant predictor of nest-box choice in
623 females (a), whereas mate retention was a significant predictor of nest-box choice in males
624 (b). The null model fit the data on mate choice by females (a), but nest-box reuse was a
625 significant predictor of mate choice in males (b).

626

TABLES

627 **Table 1 – Definition of variables**

628 Definition and nature of variables analysed in white-rumped swallows breeding in
629 Chascomús, Argentina, between 2003 and 2015.

630

Variable	Definition and nature
Nest-box choice	Categorical variable with two levels: 'reuse': occupancy by an individual in season $t + 1$ of the same box used in season t ; or 'change': occupancy in season $t + 1$ of a different box than the used in season t .
Mate choice	Categorical variable with two levels: 'retention': mating by an individual in season $t + 1$ with the same mate chosen in season t , or 'divorce': mating in season $t + 1$ with a different mate than in season t .
Age	Age of an individual in years; continuous variable (range: 2 - 7). Birds born at the Chascomús colony (i. e. recruits) had a known age. Minimum age of birds captured as adults for the first time was attributed considering that natal dispersal tends to be much greater than breeding dispersal (Bulit and Massoni 2011), assuming that they were born the previous year in a different location (i. e., were one year old at the time of banding).
Number of fledglings	Proxy of previous season reproductive performance. Number of fledglings fledged at a given nest in a given breeding season; continuous variable (range: 0-6). We did not standardized this variable with respect to the average of the colony because we assumed that individuals could more heavily weight their own breeding performance rather than comparing themselves to other birds.
Year	Year of a given observation; categorical variable with twelve levels (2003-2015, except 2012).

631 **Table 2 – Predictors of nest-box choice and mate choice**

632 Predictors of variation in nest-box choice and mate choice in white-rumped swallows breeding in Chascomús, Argentina, between
 633 2003 and 2015. Standardised coefficient estimates \pm standard errors (SE) and 95% confidence intervals (CI) are given for the best-fit
 634 model for each dataset. No effect estimates are given when the best model was the null model.

Dataset	<i>n</i>	Response	Predictor†	Estimate \pm SE	95% CI
(a) Females	241	Nest-box choice	No. of fledglings	0.32 \pm 0.12	0.04 – 0.29
		<i>Binomial</i>			
(b) Males	104	Nest-box choice	Null model	-	-
		<i>Binomial</i>			
(c) Females	92	Nest-box choice	No. of fledglings	0.31 \pm 0.18	0.09 – 0.34
		<i>Binomial</i>	Mate choice (switch)	-1.40 \pm 0.50	-6.49 – -1.14
(d) Males	96	Nest-box choice	No. of fledglings	0.99 \pm 1.32	-1.03 – 2.32
		<i>Binomial</i>	Mate choice (switch)	-7.86 \pm 2.23	-35.27 – -10.03
(e) Females	92	Mate choice	Null model	-	-
		<i>Binomial</i>			
(f) Males	96	Mate choice	Nest-box choice	-1.51 \pm 0.60	-5.36 – -0.65
		<i>Binomial</i>	(reuse)		

635 †Better fitting models had AIC values of: a) 332.5; b) 148.6, c) 117.5 , d) 109.8, e) 54.2 , and f) 93.1.

636