

## Female mate choice based on territory quality in barn swallows

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28 **Female mate choice based on territory quality in barn swallows**

29

30 **Abstract** Female mate choice based on territory quality is difficult to study because  
31 territories often contain many resources, which are difficult to quantify. Here, using the  
32 barn swallow (*Hirundo rustica gutturalis*) breeding at an outdoor breeding site in Japan,  
33 where each male defend only a small territory containing old nests, we studied whether  
34 females choose social mates based on territory quality. Since the territories of this  
35 species contain few other resources, territory quality can easily be assessed by  
36 quantifying old nests in the territory. We made the following three observations: (1)  
37 Male swallows displayed old nests in their territories to females. (2) The old nests used  
38 for first clutch were less broken than the other old nests within the same territory. (3)  
39 Territory quality, defined by the number of old nests weighted by the intactness of each  
40 old nest, predicted the productivity of the territory. (4) Males with better territories  
41 paired with females earlier, and hence bred earlier, than those with inferior territories.  
42 The relationships remained significant even after controlling for male morphological  
43 traits. Based on these results, we can infer that female swallows choose their mates  
44 based, in part, on territory quality.

45

46 **Keywords:** *Hirundo rustica gutturalis*, mate preference, mating advantage, old nests,  
47 territory choice.

48

49

49 **Introduction**

50

51 For bird species in which males defend breeding territories, females may choose mates  
52 based on male phenotype and/or territory characteristics (e.g., Alatalo et al., 1986;  
53 Buchanan & Catchpole, 1997; Marchetti, 1998; Eckerle & Thompson, 2006; reviewed  
54 in Andersson, 1994; Jennions et al., 1997; Candolin, 2003). Among such species, there  
55 have been many studies on female mate choice for male phenotype, because this  
56 promotes intersexual selection (Andersson, 1994). Female mate choice for territory  
57 characteristics should also facilitate sexual selection by promoting male-male  
58 competition and indirect mate choice (Wiley & Poston, 1996). However, female mate  
59 choice based on territory quality is less well studied owing to the difficulty of  
60 measuring territory quality in species with all-purpose territories containing many  
61 resources that are difficult to quantify (e.g., vegetation type and density, perch site, food,  
62 and nest site; Searcy & Yasukawa, 1995).

63         The barn swallow (*Hirundo rustica*) is a monogamous species in which each  
64 male defend only a small territory, which usually contain old nests constructed in  
65 previous seasons (reviewed in Møller, 1994; Turner, 2006). After pairing, pairs often  
66 repair old nests and use them as breeding nests, although they can also construct new  
67 nests (Møller, 1994). Since their territories contain few other resources, territory quality  
68 can easily be assessed by quantifying old nests in the territory. Individual old nests were  
69 in fact assessed by females or settling pairs and old nests of high quality were reported  
70 to be preferred (e.g., fewer mites; Barclay, 1988; Møller, 1990a; Safran, 2006),  
71 indicating that old nests are important resources for breeding. However, previous  
72 studies have been focused on nest choice but not on mate choice based on territory  
73 quality. It should be noted that nest choice is not equivalent to mate choice in this  
74 species. For example, even without mate choice, nest choice can be explained, because  
75 females can choose nests within territories which often contain multiple old nests or

76 nest sites in this species (cf. Barclay, 1988; the current results). In addition, nest choice  
77 can be done after pairing (cf. Møller, 1990a), which by definition does not accompany  
78 mate choice. Settling pairs may choose old nests which are not occupied by other birds.  
79 Therefore, it remains unclear whether individual males are chosen based on territory  
80 quality in the population or breeding site (but see Safran, 2007 for the influence of  
81 breeding site selection on mate choice).

82 Møller (1990b) has indirectly investigated the importance of territory quality  
83 for female mate choice from correlation analysis of settlement patterns of males in  
84 different years. The prediction is that arriving males should tend to occupy the same  
85 territories first each year if territory quality is important in determining female choice.  
86 This prediction rests on the assumption that the quality of territories remains unaltered  
87 during the period of study, as seems to be the case in his study area (Møller, 1994).  
88 Since the correlation between settlement orders in different years was low and  
89 non-significant even after excluding males that have already bred once in a study site  
90 (Møller, 1990b), he argued that territory quality is unimportant for female mate choice  
91 in barn swallows.

92 However, choosing a male as a function of the territory he is defending has  
93 three potential advantages, even if territories contain few resources other than old nests.  
94 First, since the old nests constructed in previous breeding seasons can persist and  
95 indicate past reproductive success in the territory (Safran, 2004; Turner, 2006), it would  
96 be beneficial for females to choose a breeding site based on old nests for successful  
97 breeding (Shields et al., 1988; see also Erckmann et al., 1990; Gergely et al., 2009).  
98 Indeed, Safran (2004, 2007) shows that female swallows prefer to breed in colonies  
99 containing many old nests, suggesting the importance of old nests as an indicator of  
100 breeding site quality. Second, by using old nests, females can save time by not having to  
101 build a new nest (reviewed in Turner, 2006). Although the time saving may be a small  
102 part of the whole season, starting each brood as early as possible may help improve the

103 long-term survival of the chicks and thus their chances of recruiting into the population  
104 (Turner, 2006; Gruebler & Naef-Daenzer, 2010). Early breeders are also more likely to  
105 have time for a second brood (Møller, 1994). In addition, since the re-use of old nests  
106 necessitates fewer trips to collect nesting materials, it can also reduce the risk of  
107 predation and saves energy (cf. Withers, 1977). More intact the old nest is used, more  
108 time and energy will be saved. Third, the presence of multiple old nests in a territory,  
109 which is often seen in outdoor breeding sites (compared with indoor breeding sites such  
110 as stables), may be an additional advantage for females choosing a male territory, since  
111 multiple nests may lead to a dilution effect in predation risk (cf. Watts, 1987; Searcy &  
112 Yasukawa, 1995). Multiple old nests might also be an option to breed a second clutch  
113 when the breeding nest used for a first clutch should not be used for a second clutch (e.g.  
114 increased parasite load: Møller, 1990a). Hence, we predict that female swallows choose  
115 their mates based on the intactness and quantity of old nests in male territories.

116 Old nests entailed potential costs, too. Increased ectoparasite infestation and  
117 falling nests were reported to be such costs in this species, both of which increase  
118 nestling mortality (Shields & Crook, 1987; Møller, 1990a). However, the costs of  
119 ectoparasite infestation and nest falling would not outweigh the potential benefits stated  
120 above (cf. Safran, 2006). In our study population at Joetsu city in Japan, most nest  
121 failure were from nest predation, and nestling death due to heavy infestation and nest  
122 falling were rarely found (Tajima & Nakamura, 2003; Hasegawa, 2005; M. Hasegawa,  
123 unpublished data), supporting Safran's point of view.

124 Here, we studied female mate choice based on territory quality in barn  
125 swallows nesting in an outdoor breeding site. For this purpose, we studied (i) male  
126 courtship behavior, in which important criteria of female mate choice must be shown by  
127 males (cf. Searcy & Yasukawa, 1995); (ii) nest choice within territories; (iii) the  
128 predictability of the previous productivity in territory; (iv) the relationship between  
129 breeding date (pairing date and laying date) and territory quality, defined by the number

130 of old nests weighted by the intactness of each old nest. The barn swallow is a model  
131 species for studying female mate choice or similar intersexual selection process on male  
132 phenotypes (morphological traits including coloration; Møller, 1988; Safran & McGraw,  
133 2004; body condition; Kojima et al., 2009; male nest building behaviour after pairing;  
134 Soler et al., 1998). Thus, we also investigated (v) whether female mate choice based on  
135 territory quality was confounded by male morphology including four ornaments (tail  
136 length, white spots in the tail, throat coloration, throat patch size), which might be  
137 targets of female choice in our population (Hasegawa et al., 2010a, b).

138

## 139 **Materials & methods**

140

### 141 *Study site and observations*

142

143 This study was conducted in March to August 2007 in a residential area of Joetsu City,  
144 Niigata Prefecture, Japan (37°07'N, 138°15'E; 10 m asl.), where the swallows nest  
145 under the eaves of a covered sidewalk along the street and breed in a loose colony (cf.  
146 Tajima & Nakamura, 2003). We inspected nests every other day to record breeding  
147 events. This allowed us to determine the laying date, which was expressed as the date of  
148 clutch initiation. Laying date can be used as an indicator of female mate choice (cf.  
149 Andersson, 1994; Møller, 1994). Since laying date may be influenced by a number of  
150 factors other than female choice (e.g., female quality, time required for repairing old  
151 nests, weather conditions between mating and egg laying), we also used a more direct  
152 indicator of female choice, namely, pairing date, using previously marked birds. Pairing  
153 date was defined as the first day the pair was seen together by daily observation. By  
154 daily observation, we also recorded arrival date of males (cf. Arai et al., 2009), which  
155 may be confounded with the relationship between pairing date and territory quality.

156

157 *Observing courtship behavior*

158

159 We observed each unmated male for at least one hour in front of its territory using a  
160 video camera-recorder (SONY CCD-TRV92). A total of 251 courtship displays  
161 performed by 43 unmated males (number of display for each individual, mean  $\pm$  SD = 5  
162  $\pm$  6; total observation hour: 93 h) were observed from late March to early May.

163

164 *Measuring territory quality*

165

166 In the current study, a territory was defined as the eave of one house. This is because the  
167 preliminary study showed that it was rare for more than one pair of swallows to breed  
168 under each eave in our study site (3 out of 111 in 2005 and 4 out of 97 in 2006; M.  
169 Hasegawa, unpublished data). In 2007, all but one eave had a single breeding pair (after  
170 pair formation, one pair migrated from their original territory to an eave where another  
171 pair was already breeding, probably because of human disturbance). Each eave across  
172 the study site has a similar area (ca. 10–15 m<sup>2</sup>). Before the arrival of the birds, all the  
173 nests in the study area were scored according to one of the following five categories:  
174 1—trace of old nest with little mud remaining; 2—small mass of mud remaining;  
175 3—approximately half of the old nest remaining; 4—old nest with some damage;  
176 5—old nest with little damage. Although categories 1 and 2 are rarely treated as old  
177 nests in previous studies, even these ‘scars’ would offer important information to  
178 females making decisions about where to breed (Shield et al., 1988; Safran, 2004).  
179 Territory quality was defined by the number of old nests weighted by the intactness of  
180 each old nest (i.e. if territory includes two old nests, scored 3 and 4, respectively,  
181 territory quality was  $1 \times 3 + 1 \times 4 = 7$ ). When multiple nests were found clinging together,  
182 we classified these as a single old nest and assigned it the score of the individual nest  
183 with the highest score. The reason why we used the number weighted by the intactness  
184 of each old nest is that we predicted that intactness would have influence on female  
185 choice (see Introduction section). In fact, the preliminary analyses showed that all the  
186 relationships were stronger when we used weighted sum rather than when we used the  
187 number of old nests itself. Weighted sum might not be a good measure when there are



188 many territories with many broken (i.e. score 1 or 2) old nests (e.g. 2+2+2+2+2),  
189 because the quality of such territories is judged better than the territories containing an  
190 old nest with little damage (scored 5). However, these cases were very rare in the  
191 current sample, because all territories except for three (2+2+2+2, 1+1+1+1+2, and  
192 1+1+2) include less than three broken nests (N = 67). Moreover, the analyses excluding  
193 the three territories provides qualitatively similar significant results, indicating that the  
194 influence of these cases were small. Although the above argument was based on the  
195 assumption that territories including an old nest with little damage must be better  
196 quality than territories with many broken old nests, we could not know the relative  
197 importance of intactness and quantity of old nests. Thus, we presented the analyses  
198 including the three males. Since all the three territories were held by age-unknown  
199 males, the analyses of ASY (see below) males include no such cases.

200

#### 201 *Productivity of territory*

202

203 To know the predictability of productivity by the territory quality, we investigated the  
204 relationship between territory quality and the total number of fledgling in the territory  
205 during the previous season. For this purpose, we used territories which were occupied in  
206 both 2006 and 2007. In addition, we studied the relationship between territory quality  
207 and the number of successful clutches and mean fledglings per clutch.

208

#### 209 *Capture and measurement of birds*

210

211 Adults were captured using sweep nets while roosting at night. Birds were fitted with a  
212 numbered aluminum ring and an individual combination of two or three colored rings  
213 (cf. Arai et al., 2009). The sex of an individual was determined by the presence (female)  
214 or absence (male) of an incubation patch. Adults were placed into two groups—ASY  
215 (after second year) birds and age-unknown birds—based on ringing records. Nest  
216 ownership was subsequently determined using binoculars.

217

At capture, we measured tail length, the size of the white spots in the tail, and

218 throat patch height, and collected some throat feathers. Tail length was defined as the  
219 right outermost tail feather and was measured to the nearest 0.01 mm. The size of the  
220 white spots in the tail was defined as the sum of the length of the white spots of the 2  
221 outermost tail feathers on the right side (Hasegawa et al., 2010a, b). We also recorded  
222 male body weight. Although the previous study used body condition, defined as a  
223 residual from regression of the body weight to tarsus length (Kojima et al., 2009;  
224 Hasegawa et al., 2010a), we used body weight itself as a variable because of no  
225 significant relationship between body weight and tarsus length in the current sample ( $N$   
226 = 25,  $r = 0.12$ ,  $p = 0.56$ ).

227         Throat patch height was defined as the height of the swallow's red throat patch.  
228 We used throat patch height rather than throat patch area in the current study for ease in  
229 measurement. We placed a transparent plastic sheet on the throat region, ensuring that  
230 the feathers lay flat in their natural position, and traced the size of the patch on the sheet  
231 with a marker pen (cf. Lendvai et al., 2004). We scanned the sheet and measured the  
232 height of the patch (in millimeters) by using Scion Image software (Scion Corporation,  
233 Frederick, MD). For each bird, throat patch was traced twice and the mean of the 2  
234 measurements was used. The detailed method is described elsewhere (Hasegawa et al.,  
235 2010a).

236         Once in the laboratory, we piled five feathers on a piece of white paper so that  
237 the perimeters of the feathers coincided. The feather samples were scanned at 800-dpi  
238 resolution by using an EPSON GT 9300 UF scanner, and the images obtained were  
239 imported into the Adobe Photoshop Elements 3.0 program (Adobe Systems, USA). We  
240 measured mean RGB values in a square of 30 pixels near the distal end of the feather  
241 sample. The mean RGB values were converted to hue-saturation-brightness  
242 (HSB)-values by the algorithm described by Foley & van Dam (1984). Among these  
243 three color variables, saturation value is taken as the representative of plumage  
244 coloration, because this variable does not need to be corrected for plumage color fading

245 (Hasegawa et al., 2008). The detailed method is described elsewhere (Hasegawa et al.,  
246 2008, 2010a). RGB color systems and subsequent conversion into HSB is commonly  
247 used for measuring feather coloration, especially when there is no reflectance in  
248 ultraviolet region (reviewed in Hill & McGraw, 2006), which is also the case in the  
249 throat feathers of barn swallows (Safran & McGraw, 2004; M Hasegawa, unpublished  
250 data).

251

### 252 *Statistical procedures*

253

254 To compare the nest scores between a used nest for first clutch and the other old nests  
255 within each territory, we used a liner mixed-effect model (LME) using the function lme  
256 (package nlme) in the R statistical package (version 2.8.0; R Development Core Team,  
257 2008). This is similar procedure with paired *t*-test, but can compare more than two nests  
258 within each territory differed with paired *t*-test. Since the data were overdispersed, we  
259 used a general linear model (GLM) using a quasi-poisson error distribution and a log link  
260 function to investigate pairing date and laying date in relation to territory quality.

261 Among the breeding pairs, only one pair bred in a territory without old nests (1/84). We  
262 excluded this pair from the analysis, although their inclusion did not affect the results.

263 This pair was excluded from the analysis so as not to confound the quantitative  
264 difference of old nests in the territory with the effect of the presence of old nests. Since  
265 laying date is known to be affected by male age, analyses were also conducted using  
266 only ASY males to distinguish the effect of male age from that of territory quality itself.  
267 Since laying date may be affected by male morphological traits, analyses were also  
268 conducted after statistically controlling for significant effects of male morphological  
269 traits. We obtained pseudo- $R^2$  values (in the following simply referred to as  $R^2$ ) as a  
270 measure of variance accounted for by the model (Heinzel & Mittlböck, 2003). All data  
271 analyses were performed using the R statistical package.

272

## 273 **Results**

### 274 *Courtship behavior*

275

276 Among 251 courtship displays observed, most males commenced courtship in the air (N  
277 = 208) while the others started courting on telegraph wires (N = 43). Secondly, they led  
278 females to an old nest or to a potential nest site (N = 182), which contained no old nest  
279 but could be used to construct a new nest, emitting typical “*wie-wie-wie*” notes (cf.  
280 Turner, 2006). Thirdly, approximately one-half of the males that successfully led  
281 females to a nest (34 out of 69) were also observed to sequentially show females other  
282 nests in their territories.

283

### 284 *Nest choice within a territory*

285

286 Each territory contained  $2.09 \pm 1.04$  old nests (mean  $\pm$  SD; range = 1–5 nests;  $N = 67$ ).  
287 When the nest scores of nests used for first clutch among pairs that had at least two old  
288 nests in their territory were compared with the scores of the other old nests within the  
289 same territory, old nests used for first clutch were found to have significantly higher  
290 scores (LME: the random factor is territory ID;  $N_{\text{territory}} = 36$ ,  $N_{\text{nest}} = 91$ , Coef  $\pm$  SE =  
291  $0.77 \pm 0.30$ ,  $t = 2.54$ ,  $p = 0.01$ ).

292

### 293 *Territory quality and productivity*

294

295 Population means of territory quality, defined by the number of old nests weighted by  
296 the intactness of each old nest was  $7.45 \pm 3.57$  (mean  $\pm$  SD, range from 2 to 18;  $N = 67$ ).  
297 Territory quality was positively correlated with the total number of fledglings in the  
298 territory during the previous year ( $N = 47$ , Spearman’s rank correlation coefficient,  $r_s =$

299 0.44,  $p < 0.01$ ; Fig. 1). This relationship remained significant even after excluding an  
300 outlier ( $N = 46$ ,  $r_s = 0.41$ ,  $p < 0.01$ ). The significant relationship derived from the  
301 positive relationship between territory quality and the number of successful clutches  
302 (range from 0 to 2;  $N = 47$ ,  $r_s = 0.55$ ,  $p < 0.01$ ). There was no significant relationship  
303 between territory quality and mean fledgling number per clutch (range from 0 to 5;  $N =$   
304  $47$ ,  $r_s = 0.11$ ,  $p = 0.48$ ).

305

### 306 *Territory quality and laying date*

307

308 There was a negative relationship between territory quality and laying date ( $N = 67$ ,  
309  $\text{Coef} \pm \text{SE} = -0.07 \pm 0.03$ ,  $F = 8.90$ ,  $R^2 = 0.11$ ,  $p = 0.004$ ; open and filled circles and  
310 broad regression curve in Figure 2). Since there were effects of male age on laying date  
311 (ASY males:  $N = 22$ , median = 20 April, range = 12 April to 8 May; age-unknown  
312 males:  $N = 58$ , median = 2 May, range = 13 April to 8 June; Mann-Whitney  $U$ -test,  $z =$   
313  $3.85$ ,  $p < 0.0001$ ) and on territory quality (ASY males:  $N = 21$ , mean  $\pm$  SE =  $9.0 \pm 0.8$ ;  
314 age-unknown males:  $N = 46$ , mean  $\pm$  SE =  $6.8 \pm 0.5$ ; Mann-Whitney  $U$ -test,  $z = 2.52$ ,  $p$   
315  $= 0.01$ ), age effects might have confounded the results. However, this was not the case,  
316 because the effect of territory quality remained even after excluding males whose age  
317 was not known (GLM with quasi-poisson distribution:  $N = 21$ ,  $\text{Coef} \pm \text{SE} = -0.12 \pm 0.04$ ,  
318  $F = 10.74$ ,  $R^2 = 0.29$ ,  $p = 0.004$ ; filled circles and narrow regression curve in Figure 2).  
319 This relationship remained significant even when using males that did not reunite with  
320 their mate of the previous year (GLM with quasi-poisson distribution:  $N = 14$ ,  $\text{Coef} \pm \text{SE}$   
321  $= -0.13 \pm 0.05$ ,  $F = 7.66$ ,  $R^2 = 0.36$ ,  $p = 0.02$ ).

322

323 In ASY males, it is possible that females use the productivity of territory  
324 directly by observing fledgling number in the previous years instead of using territory  
325 quality which is an indirect indicator of the productivity. Thus, we studied the  
relationship between the productivity of the territory during the previous year and laying

326 date. However, laying date was not significantly related to the total number of  
327 fledglings in the territory during the previous year and laying date (GLM with  
328 quasi-poisson distribution;  $N = 16$ ,  $\text{Coef} \pm \text{SE} = -0.01 \pm 0.09$ ,  $F = 0.02$ ,  $R^2 = -0.07$ ,  $p =$   
329  $0.90$ ), nor the number of successful clutches (GLM with quasi-poisson distribution;  $N =$   
330  $16$ ,  $\text{Coef} \pm \text{SE} = -0.13 \pm 0.31$ ,  $F = 0.17$ ,  $R^2 = -0.06$ ,  $p = 0.69$ ).

331

### 332 *Territory quality and pairing date*

333

334 We also found a negative relationship between pairing date and territory quality in ASY  
335 birds (GLM with quasi-poisson distribution:  $N = 18$ ,  $\text{Coef} \pm \text{SE} = -0.18 \pm 0.07$ ,  $F = 9.29$ ,  
336  $R^2 = 0.30$ ,  $p = 0.007$ ; Figure 3). This relationship remained significant even when using  
337 males that did not reunite with their mate of the previous year (GLM with quasi-poisson  
338 distribution:  $N = 13$ ,  $\text{Coef} \pm \text{SE} = -0.16 \pm 0.07$ ,  $F = 6.81$ ,  $R^2 = 0.28$ ,  $p = 0.02$ ). There  
339 was a similar relationship between pairing date and territory quality after controlling for  
340 arrival date (GLM with quasi-poisson distribution:  $N = 18$ ; territory quality:  $\text{Coef} \pm \text{SE} =$   
341  $-0.15 \pm 0.07$ ,  $F = 5.52$ ,  $p = 0.03$ ; arrival date:  $\text{Coef} \pm \text{SE} = 0.06 \pm 0.03$ ,  $F = 4.03$ ,  $p =$   
342  $0.06$ ; overall model:  $F = 7.11$ ,  $R^2 = 0.40$ ,  $p < 0.01$ ), indicating that differential arrival  
343 date was not confounded with the significant relationship between territory quality and  
344 pairing date. Among the 18 males for which the pairing date was known, four males  
345 changed their territory before their mating status was confirmed (i.e., unmated or mated).  
346 Hence, it is possible that some of these birds changed breeding territory after pair  
347 formation. However, excluding these four birds did not alter the relationship between  
348 pairing date and territory quality (GLM with quasi-poisson distribution:  $N = 14$ ,  $\text{Coef} \pm$   
349  $\text{SE} = -0.18 \pm 0.05$ ,  $F = 13.62$ ,  $R^2 = 0.46$ ,  $p = 0.003$ ). This was also the case when  
350 controlling for the effect of arrival date (GLM with quasi-poisson distribution;  $N = 14$ ;  
351 territory quality:  $\text{Coef} \pm \text{SE} = -0.14 \pm 0.06$ ,  $F = 7.29$ ,  $p = 0.02$ ; arrival date:  $\text{Coef} \pm \text{SE} =$   
352  $0.03 \pm 0.02$ ,  $F = 1.94$ ,  $p = 0.19$ ; overall model:  $F = 7.95$ ,  $R^2 = 0.50$ ,  $p < 0.01$ ).

353 Mating date was not significantly related to the total number of fledglings in  
354 the territory during the previous year (GLM with quasi-poisson distribution;  $N = 12$ , Coef  
355  $\pm$  SE =  $-0.02 \pm 0.14$ ,  $F = 0.03$ ,  $R^2 = -0.08$ ,  $p = 0.87$ ) and the number of successful  
356 clutches (GLM with quasi-poisson distribution;  $N = 12$ , Coef  $\pm$  SE =  $-0.26 \pm 0.52$ ,  $F =$   
357  $0.24$ ,  $R^2 = -0.07$ ,  $p = 0.63$ ), although sample sizes were small.

358

### 359 *The influence of male morphology*

360

361 Among seven male morphological traits, wing length, tail length, and white spots in the  
362 tail were significantly correlated with laying date (Table 1). Thus, the relationship  
363 between laying date and territory quality might be confounded by these variables.  
364 However, this might not be the case, because territory quality remained significant even  
365 after controlling for these three significant terms separately or in combination (territory  
366 quality:  $N = 31$ , Coef  $> -0.08$ ,  $F > 5.29$ ,  $p < 0.03$ ).

367 In ASY males, none of seven morphological characters were significantly  
368 correlated with laying date (Table 1). Thus, male morphology might not be confounded  
369 with the significant relationship between territory quality and laying date in ASY males.  
370 This was also the case for the analysis of pairing date (Table 1).

371

## 372 **Discussion**

373

374 In this study, we showed that males displayed old nests to females during their courtship  
375 behavior, suggesting the importance of old nests in attracting potential mates. Within  
376 territories, more intact old nests were used as breeding nests. Territory quality, defined  
377 by the number of old nests weighted by the intactness of each old nest, provided  
378 information about the productivity of the territory (Figure 1). Males having many intact  
379 old nests in their territory bred earlier than others (Figures 2 & 3). These results are

380 consistent with the idea that female barn swallows chose their social mates, in part,  
381 based on territory quality. Since we used the intactness of old nests as the criterion of  
382 territory quality, the early laying date in good territories may be attributable to the fact  
383 that pairs in these territory spend less time repairing old nests before laying a clutch  
384 than those in less good territories (e.g., Turner, 2006; Safran, 2006). However, this  
385 explanation could not account for the early mating date of males with good territories  
386 (Figure 3). The alternative explanation that females chose territory indirectly from male  
387 ornaments might not be the case, because female mate choice based on territory quality  
388 remains significant after controlling for male ornaments. These analyses could not deny  
389 the possibility that territory quality was correlated with some other male traits (e.g. song,  
390 courtship performance), which was directly chosen by females. However, even in these  
391 cases, females indirectly chose males based on territory quality as a result. Thus, we  
392 conclude that female swallows choose their mates based on territory quality.

393         Our finding is inconsistent with the argument that territory quality is  
394 unimportant for mate choice in barn swallows in another population (Møller, 1990b,  
395 1994). Møller's argument is based on the observation that the correlation between  
396 settlement orders in different years was low and non-significant, which should be  
397 positively correlated if territory quality is important. However, his argument rests on  
398 some assumptions (see Introduction section; see also Møller, 1994) and is not a  
399 necessary condition for female mate choice based on territory quality. Thus, although  
400 their study did not find evidence of female mate choice for territory quality, we could  
401 not determine whether the difference in conclusion between Møller's and ours is for the  
402 difference of methodology or population difference in female behavior itself (see  
403 below). Anyway, to the best of our knowledge, the current study is the first to show  
404 female mate choice based on territory quality in barn swallows. This study reinforces  
405 the previous finding that females or settling pairs choose their breeding site (colony  
406 choice: Safran, 2004, 2007; breeding nests: Barclay, 1988; Møller, 1990a; Safran, 2006),



407 and further demonstrates that females use similar criteria when choosing their mates.  
408 Since old nests provide several benefits, all of which increased fitness of females, and  
409 some costs (reviewed in Introduction; Turner, 2006), it might be beneficial for females  
410 to choose proper breeding site when choosing nest and colony themselves as well as  
411 choosing males having different quality of territories.

412 As shown in this study, even females of a species that has few resources other  
413 than nests within its territory choose their mates based on territory quality. Female mate  
414 choice based on territory quality, measured by nest-site quality, has also been shown in  
415 certain other species (e.g., pied flycatcher: Slagsvold, 1986; house sparrow: Møller,  
416 1988). Thus, territories containing few resources other than nests should not simply be  
417 assumed to be unimportant, which has been the case in some studies (e.g., Møller, 1994;  
418 Carty et al., 1999; Friedl & Klump, 1999). Rather, since the measure of nest site, such  
419 as the quality of old nests, can be easily quantified both by observers and birds and was  
420 often used for nest site choice (e.g. Erckmann et al., 1990; Antonov & Atanasova, 2003;  
421 Mazgajski, 2007; Gergely et al., 2009), species with territory which include few  
422 resources other than nests should be used as model species to study female mate choice  
423 based on territory quality.

424 Here, we showed female mate choice based on territory quality in the barn  
425 swallow, which is a model species for sexual selection (Møller, 1994). Sexual selection  
426 studies for male ornaments in this species have focused exclusively on female mate  
427 choice (reviewed in Møller, 1994). However, female mate choice based on territory  
428 quality was relatively more important than male ornaments in the given environment  
429 and thus could have an influence on sexual selection by promoting male-male  
430 competition and indirect mate choice for male phenotype (Wiley & Poston, 1996).  
431 Sexual selection studies should take territory quality into consideration to know how the  
432 selection works on male phenotype, which is beyond our scope here. In addition, the  
433 intensity and direction of female mate choice based on territory quality may vary among

434 populations, which is predicted from geographic variation in the relative importance of  
435 benefits and costs of old nests (e.g. the importance of ectoparasite would differ among  
436 populations; Barclay, 1988; Safran, 2006). It remains to be determined whether female  
437 mate choice based on territory quality varies across species range and its influence on  
438 the geographic variation in sexual selection and ornamentation.

439

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444

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548 **Table 1** Simple GLM with quasipoisson distribution between male morphological traits and the laying date (12  
 549 April = 0) of his mate and pairing date (31 March = 0) of his mate.

	Laying date (All males)		Laying date (ASY males)		Pairing date (ASY males)	
	<i>N</i> = 31		<i>N</i> = 17		<i>N</i> = 15	
	Coefficient	<i>R</i> <sup>2</sup>	Coefficient	<i>R</i> <sup>2</sup>	Coefficient	<i>R</i> <sup>2</sup>
Wing length	-0.31 ±0.14 (0.03)	0.12	-0.19 ±0.18 (0.31)	0.00	-0.28 ±0.36 (0.44)	-0.03
Tarsus length	-0.26 ±0.15 (0.08)	0.07	-0.03 ±0.20 (0.87)	-0.07	0.07 ±0.30 (0.81)	-0.07
Body mass <sup>1</sup>	-0.22 ±0.14 (0.12)	0.06	-0.16 ±0.21 (0.45)	-0.04	-0.28 ±0.43 (0.52)	-0.06
Throat patch height	-0.18 ±0.14 (0.20)	0.02	0.11 ±0.20 (0.59)	-0.05	0.13 ±0.31 (0.68)	-0.06
Throat coloration	0.23 ±0.16 (0.15)	0.04	0.25 ±0.20 (0.21)	0.04	0.41 ±0.36 (0.25)	0.03
Tail length	-0.45 ±0.13 (<0.01)	0.26	-0.05 ±0.20 (0.82)	-0.06	0.20 ±0.44 (0.65)	-0.06
Size of the white spots in the tail	-0.35 ±0.14 (0.02)	0.16	-0.28 ±0.19 (0.17)	0.07	-0.21 ±0.30 (0.50)	-0.04

550 Standardized coefficient ± SE (*p*-value) of each morphological variable are shown.

551 <sup>1</sup>Sample size reduced to 25, 12, and 10, respectively.

552 Figure legends

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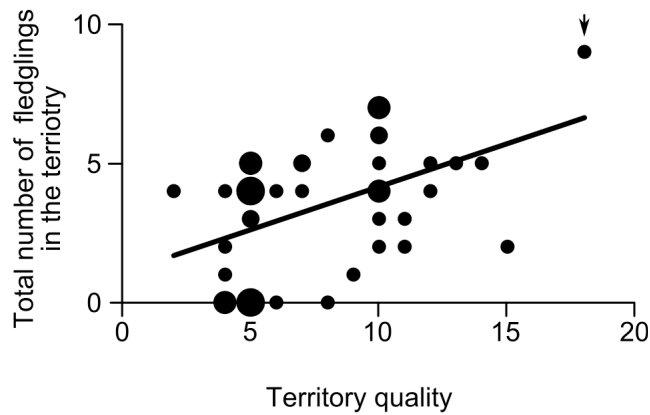
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570 **Fig. 1** Relationship between male territory quality and the total number of fledglings in the  
571 territory during the previous breeding season. Circles of increasing size represent one, two,  
572 three, and four observations, respectively. The arrow indicates an outlier. The line is the  
573 linear regression line.

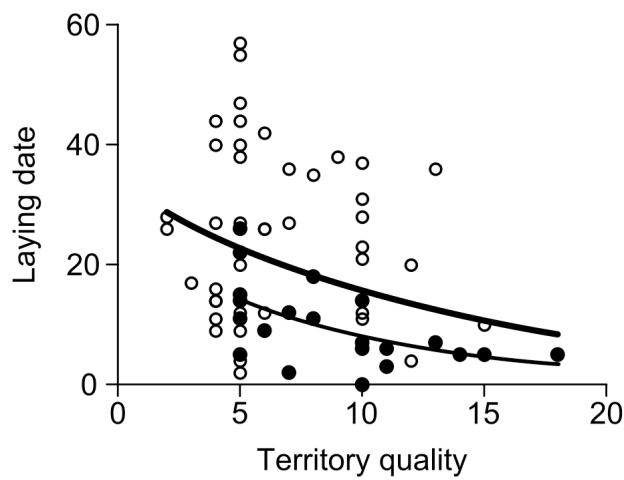
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**Fig. 2** Relationship between male territory quality and the laying date (12 April = 0) of his mate. Filled and open circles indicate ASY and age-unknown males, respectively. Regression curves, which were predicted by GLM with quasi-poisson distribution, are shown (broad line: ASY and age-unknown males; narrow line: ASY males only)

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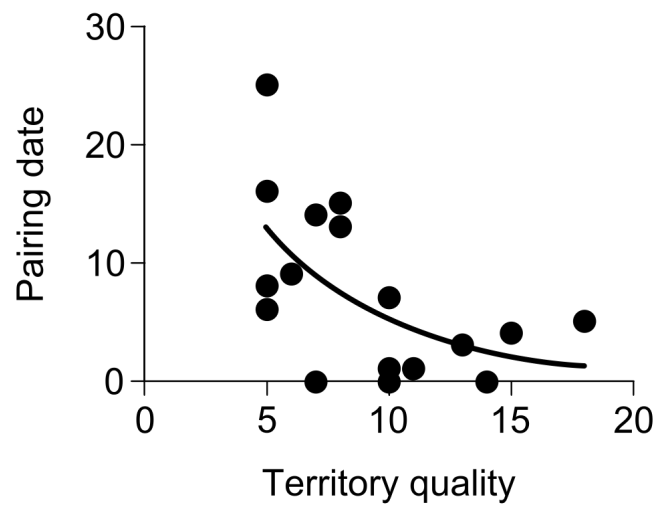
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620 **Fig. 3** Relationship between male territory quality and pairing date (31 March = 0) in ASY  
621 males. A regression curve, which was predicted by GLM with quasi-poisson distribution, is  
622 shown