Female mate choice based on territory quality in barn swallows

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

Introduction

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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

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103   long-term survival of the chicks and thus their chances of recruiting into the population

104   (Turner, 2006; Grüebler & 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 ± SD = 5

162   ± 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^2). 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 1×3+1×4 = 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

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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

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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 (Heinzl & Mittlböck, 2003). All data

271 analyses were performed using the R statistical package.

272

Results

Courtship behavior

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

Nest choice within a territory

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

Territory quality and productivity

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

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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   Coef ± SE = -0.07 ± 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 ± SE = 9.0 ± 0.8;

314   age-unknown males: $N = 46$, mean ± SE = 6.8 ± 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: $N = 21$, Coef ± SE = -0.12 ± 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: $N = 14$, Coef ± SE

321   = -0.13 ± 0.05, $F = 7.66$, $R^2 = 0.36$, $p = 0.02$).

322   In ASY males, it is possible that females use the productivity of territory

323   directly by observing fledgling number in the previous years instead of using territory

324   quality which is an indirect indicator of the productivity. Thus, we studied the

325   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; $N = 16$, Coef $\pm$ 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, Coef $\pm$ 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: $N = 18$, Coef $\pm$ SE = -0.18 ± 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: $N = 13$, Coef $\pm$ SE = -0.16 ± 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: Coef $\pm$ SE =

341   -0.15 $\pm$ 0.07, $F = 5.52$, $p = 0.03$; arrival date: Coef $\pm$ 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: $N = 14$, Coef $\pm$

349   SE = -0.18 ± 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: Coef $\pm$ SE = -0.14 ± 0.06, $F = 7.29$, $p = 0.02$; arrival date: Coef $\pm$ SE =

352   0.03 $\pm$ 0.02, $F = 1.94$, $p = 0.19$; overall model: $F = 7.95$, $R^2 = 0.50$, $p < 0.01$).

13

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

14

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

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

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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) | |
| | $N = 31$ | | $N = 17$ | | $N = 15$ | |
	Coefficient	R^2	Coefficient	R^2	Coefficient	R^2
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[1]	−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 [1]Sample size reduced to 25, 12, and 10, respectively.

552   Figure legends

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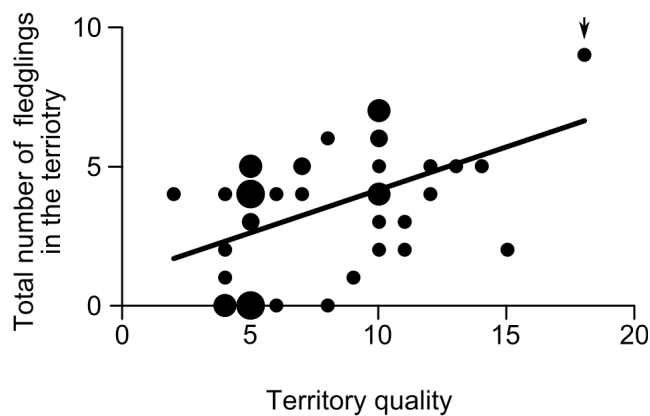559

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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

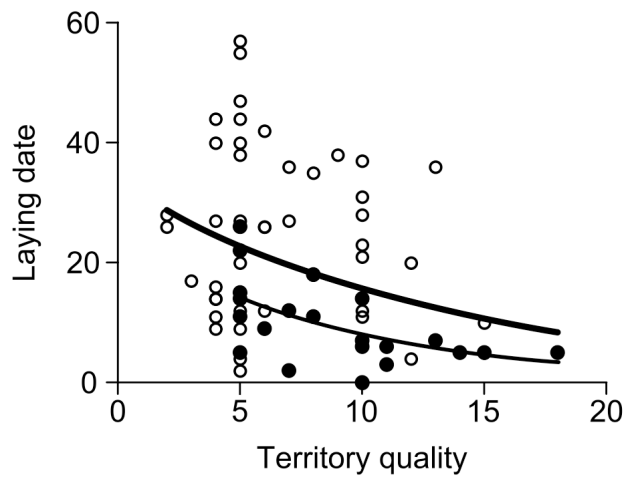573   linear regression line.

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596 **Fig. 2** Relationship between male territory quality and the laying date (12 April = 0) of his

597 mate. Filled and open circles indicate ASY and age-unknown males, respectively.

598 Regression curves, which were predicted by GLM with quasi-poisson distribution, are

599 shown (broad line: ASY and age-unknown males; narrow line: ASY males only)

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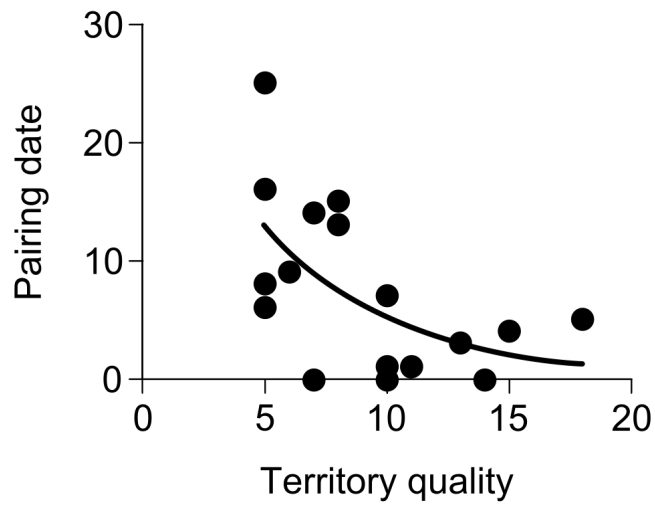
Fig. 3 Relationship between male territory quality and pairing date (31 March = 0) in ASY

males. A regression curve, which was predicted by GLM with quasi-poisson distribution, is

shown