

1
2 **Female mate choice based on territory quality**
3 **in barn swallows**
4

5
6 **Running head**

7 **Female mate choice based on territory quality**
8

9
10 Masaru Hasegawa¹ (corresponding author), Emi Arai²,
11 Mamoru Watanabe¹, & Masahiko Nakamura²
12

13 ¹Graduate School of Life and Environmental Sciences, University of Tsukuba, Tsukuba,
14 1-1-1 Tennoudai, Tsukuba-shi, Ibaraki 305-8572, Japan

15 ²Laboratory of Animal Ecology, Department of Biology, Joetsu University of Education,
16 1 Yamayashiki-machi, Joetsu-shi, Niigata 943-8512, Japan
17

18
19 Total text page 22

20 Number of tables 1

21 Number of figures 3
22

23
24 Corresponding author

25 Masaru Hasegawa

26 E-mail: perorobomusadiobe@gmail.com

27 Tel: 076-261-6075
28

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 m²). 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 (Heinzl & 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 ± 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 ± 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 ± 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 ± 0.8 ;
314 age-unknown males: $N = 46$, mean \pm 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: $N = 21$, $\text{Coef} \pm \text{SE} = -0.12 \pm 0.04$,
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 ± 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 ± 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 ± 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 ± 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 ± 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

440 **Acknowledgements** We are grateful to the residents of Joetsu City for their kind
441 support and assistance. This manuscript benefited from comments by R. J. Safran. We
442 also thank the members of the Laboratory of Animal Ecology of Joetsu University of
443 Education and the Laboratory of Conservation Ecology of University of Tsukuba.

444

445 **References**

446

- 447 Alatalo RV, Lundberg A, Glynn C (1986) Female pied flycatchers choose territory
448 quality and not male characteristics. *Nature* 323:152–153
- 449 Andersson M (1994) *Sexual selection*. Princeton University Press, Princeton
- 450 Antonov A, Atanasova D (2003) Re-use of old nests versus the construction of new
451 ones in the Magpie *Pica pica* in the city of Sofia (Bulgaria). *Acta Ornithol*
452 38:1–4
- 453 Arai E, Hasegawa M, Nakamura M (2009) Divorce and asynchronous arrival in Barn
454 Swallows *Hirundo rustica*. *Bird Study* 56:411–413
- 455 Barclay RM (1988) Variation in the costs, benefits, and frequency of nest reuse by Barn
456 Swallows (*Hirundo rustica*). *Auk* 105:53–60
- 457 Buchanan K, Catchpole C (1997) Female choice in the sedge warbler, *Acrocephalus*
458 *schoenobaenus*: multiple cues from song and territory quality. *Proc R Soc Lond*
459 B 264:521–526
- 460 Candolin U (2003) The use of multiple cues in mate choice. *Biol Rev* 78:575–595

- 461 Catry P, Phillips RA, Furness R (1999) Evolution of reversed sexual size dimorphism in
462 skuas and jaegers. *Auk* 116:158–168
- 463 Eckerle KP, Thompson CF (2006) Mate choice in house wrens: nest cavities trump male
464 characteristics. *Behaviour* 143:253–271
- 465 Erckmann WJ, Beletsky LD, Orians GH, Johnsen T, Sharbaugh S, D'Antonio C (1990)
466 Old nests as cues for nest-site selection: an experimental test with red-winged
467 blackbirds. *Condor* 92:113–117
- 468 Foley JD, van Dam A (1984) Intensity and color. In: *Fundamentals of Interactive*
469 *Computer Graphics*. Addison-Wesley, Philippines, pp 593–622
- 470 Friedl TWP, Klump GM (1999) Determinants of male mating success in the red bishop
471 (*Euplectes orix*). *Behav Ecol Sociobiol* 46:387–399
- 472 Gergely Z, Mészáros A, Szabad J, Székely T (2009) Old nests are cues for suitable
473 breeding sites in the Eurasian penduline tit *Remiz pendulines*. *J Avian Biol*
474 40:2–6
- 475 Gruebler M U, Naef-Daenzer B (2010) Fitness consequences of timing of breeding in
476 birds: data effects in the course of a reproductive episode. *J Avian Biol*
477 41:282–291
- 478 Hasegawa M (2005) *Nihonno tsubame ni okeru seisentaku keisitu*. —MS Thesis,
479 University of Tsukuba, Tsukuba, Japan (In Japanese)
- 480 Hasegawa M, Arai E, Watanabe M, Nakamura M (2008) Methods for correcting
481 plumage color fading in the Barn Swallow. *Ornithol Sci* 7:117–122
- 482 Hasegawa M, Arai E, Watanabe M, Nakamura M (2010a) Mating advantage of multiple
483 male ornaments in the Barn Swallow *Hirundo rustica gutturalis*. *Ornithol Sci*
484 9:141–148
- 485 Hasegawa M, Arai E, Kojima W, Kitamura W, Fujita G, Higuchi H, Watanabe M,
486 Nakamura M (2010b) Low level of extra-pair paternity in a population of the
487 Barn Swallow *Hirundo rustica gutturalis*. *Ornithol Sci* 9:161–164

488 Heinzl H, Mittlbock M (2003) Pseudo *R*-squared measures for Poisson regression
489 models with over- or underdispersion. *Computational Statistics and Data*
490 *Analysis* 44:253–271

491 Hill GE, McGraw KJ (2006) *Bird coloration. I. Mechanisms and measurements.*
492 Harvard Univ. Press, Cambridge.

493 Kojima W, Kitamura W, Kitajima S, Ito Y, Ueda K, Fujita G, Higuchi H (2009) Female
494 barn swallows gain indirect but not direct benefits through social mate choice.
495 *Ethology* 115:939–947

496 Jennions MD, Petrie M (1997) Variation in mate choice and mating preferences: a
497 review of causes and consequences. *Biol Rev* 72:283–327

498 Lendvai AZ, Kis J, Szekely T, Cuthill IC (2004) An investigation of mate choice based
499 on manipulation of multiple ornaments in Kentish plovers. *Anim Behav*
500 67:703–709

501 Marchetti K (1998) The evolution of multiple male traits in the yellow-browed leaf
502 warbler. *Anim Behav* 55:361–376

503 Mazgajski TD (2007) Effect of old nest material on nest site selection and breeding
504 parameters in secondary hole nesters ? a review. *Acta Ornithol* 42:1–14

505 Møller AP (1988) Badge size in the house sparrow *Passer domesticus*. *Behav Ecol*
506 *Sociobiol* 22:373–378

507 Møller AP (1990a) Effects of parasitism by a haematophafous mite on reproduction in
508 the barn swallow. *Ecology* 71: 2345–2357

509 Møller AP (1990b) Male tail length and female mate choice in the monogamous
510 swallow *Hirundo rustica*. *Anim Behav* 39:458–465

511 Møller AP (1994) *Sexual selection and the barn swallow*. Oxford University Press,
512 Oxford

513 R Development Core Team (2008) *R: A language and environment for statistical*
514 *computing*. R Foundation for Statistical Computing, Vienna, Austria. ISBN

515 3-900051-07-0; Available at www.R-project.org

516 Safran RJ (2004) Adaptive site selection rules and variation in group size of barn
517 swallows: individual decisions predict population patterns. *Amer Natur*
518 164:121–131

519 Safran RJ (2006) Nest-site selection in the barn swallow, *Hirundo rustica*: What
520 predicts seasonal reproductive success? *Can J Zool* 84:1533–1539

521 Safran RJ (2007) Settlement patterns of female barn swallows *Hirundo rustica* across
522 different group sizes: access to colorful males or favored nests? *Behav Ecol*
523 *Sociobiol* 61:1359–1368

524 Safran RJ, McGraw KJ (2004). Plumage coloration, not length or symmetry of
525 tail-streamers, is a sexually selected trait in North American barn swallows.
526 *Behav Ecol* 15:455–461

527 Searcy WA, Yasukawa K (1995) Polygyny and Sexual Selection in Red-winged
528 Blackbirds. Princeton University Press, Princeton

529 Shields WM, Crook JR (1987) Barn swallow coloniality: a net cost for group breeding
530 in the Adirondacks? *Ecology* 68:1373–1386

531 Shields WM, Crook JR, Heibblythwaite ML, Wiles-Ehmann SS (1988) Ideal free
532 coloniality in the swallows. In: Slobodchikoff CN (ed) *The Ecology of Social*
533 *Behavior*. Academic Press, San Diego, pp 189–228

534 Slagsvold T (1986) Nest site settlement by the Pied Flycatcher: does the female choose
535 her mate for the quality of his house or himself? *Ornis Scand* 17:210–220

536 Soler JJ, Cuervo JJ, Møller AP, De Lope F (1998) Nest building is a sexually selected
537 behaviour in the barn swallow. *Anim Behav* 56: 1435–1442

538 Tajima K, Nakamura M (2003) Response to manipulation of partner contribution: A
539 handicapping experiment in the Barn Swallow. *Ornithol Sci* 2: 65–72

540 Turner AK (2006) *The Barn Swallow*. T & AD Poyser, London

541 Watts BD (1987) Old nest accumulation as a possible protection mechanism against

542 search-strategy predators. *Anim Behav* 35:1566–1568
543 Wiley RH, Poston J (1996) Indirect mate choice, competition for mates, and
544 coevolution of the sexes. *Evolution* 50:1371–1381
545 Withers PC (1977) Energetic aspects of reproduction by the Cliff Swallow. *Auk*
546 94:718–725
547

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> ²	Coefficient	<i>R</i> ²	Coefficient	<i>R</i> 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 ¹Sample size reduced to 25, 12, and 10, respectively.

552 Figure legends

553

554

555

556

557

558

559

560

561

562

563

564

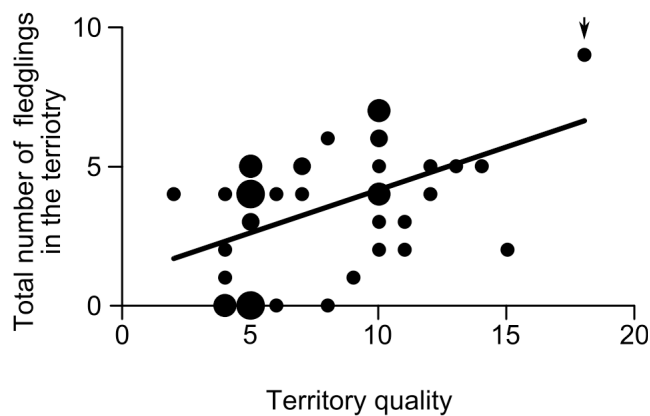
565

566

567

568

569



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.

574

575

576

577
578
579
580
581
582
583
584
585
586
587
588
589
590
591
592
593
594
595
596
597
598
599
600
601

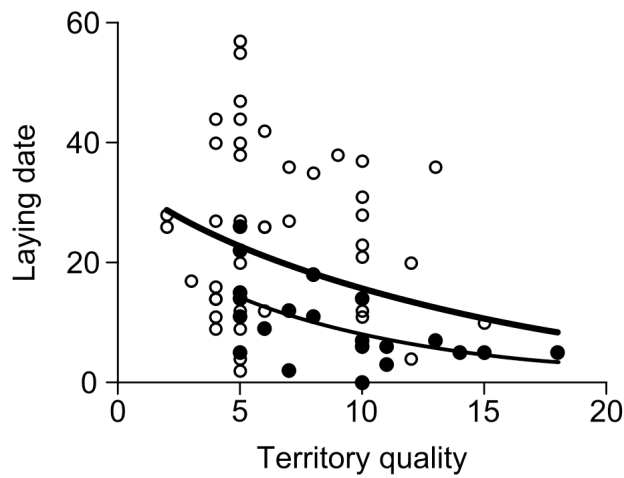
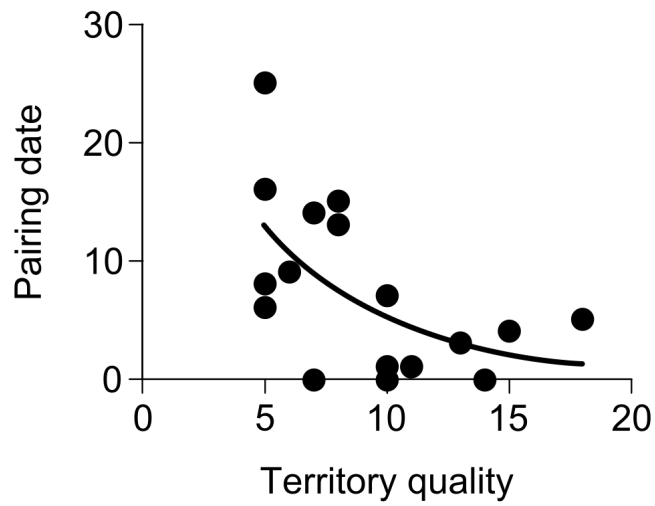


Fig. 2 Relationship between male territory quality and the laying date (12 April = 0) of his mate. Filled and open circles indicate ASY and age-unknown males, respectively. Regression curves, which were predicted by GLM with quasi-poisson distribution, are shown (broad line: ASY and age-unknown males;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

602
603
604
605
606
607
608
609
610
611
612
613
614
615
616
617
618
619



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