

1 **Marginal-covert moult in the House Sparrow *Passer domesticus***

2 Moult of marginal coverts

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## 11 **ABSTRACT**

12 Marginal coverts are often neglected in passerine moult studies due to their small size and  
13 large number. Here, we document eight moult components of this group of wing coverts in a  
14 House Sparrow population from Barcelona in 2018–2021: timing, growth rate, intensity, speed,  
15 duration, sequence, extent, and barb density. We also tested the influence of various intrinsic  
16 and extrinsic factors on marginal-covert moult. Our adult population started marginal-covert  
17 moult on 29<sup>th</sup> July and finished it on 29 August, with the moult of hatch-year birds delayed 13  
18 days in relation to the moult of adults. Growth rate of the largest marginal covert after  
19 significantly increased with its size but did not differ between sexes. Intensity of marginal-  
20 covert moult replacement was not constant during the moult progress, which took 32 days  
21 long on average. Moult sequence of marginal coverts started by the proximal feathers,  
22 proceeded distally replacing the central rows and completed toward the front and rear rows.  
23 Moult extent was complete but in one case. Size of the largest marginal covert increased with  
24 calamus width not significantly and barb density decreased with feather size not significantly,  
25 neither of which differed between sexes. Comparison with published results indicated that  
26 growth rate is lower in marginal coverts than in primaries and rectrices, whereas barb density  
27 is greater. Lineal regression of marginal-covert size on both growth rate and barb density can  
28 be used to predict growth rate and barb density of flight feathers in the House Sparrow.

29

## 30 **Introduction**

31 Moult is a physiological process whose aim is to maintain and adjust the functions of a bird's  
32 plumage (Jenni & Winkler 2020a). It consists of the replacement of an old feather by a new  
33 one: the new feather grows within a protective sheath that elongates and forces the old  
34 feather out of the follicle (Lucas & Stettenheim 1972). The deposition of material in the  
35 growing feather is thought to proceed at a nearly constant rate in passerine species (Winkler *et*

36 *al* 1988). However, the replacement of all the old feathers cannot happen simultaneously in  
37 passerines and must be coordinated to reduce plumage-function loss and avoid maladaptation  
38 (but see Haukioja 1971, Green & Summers 1975). Importantly, passerine moult has evolved to  
39 coincide with specific periods in each species' annual cycle, above all in temperate regions  
40 (Barta *et al* 2006, 2008). The moult process is active during this period, and can be quantified  
41 as a function of four time-related components: 1) the feather growth rate, the daily increase in  
42 length of a single feather, which depends on metabolic rate and has been found to correlate  
43 with environmental variables such as habitat quality (Vangestel *et al* 2010); 2) the intensity of  
44 the plumage moult, the quantity of feathers growing simultaneously, which affects plumage  
45 performance (Hedenström 1998); 3) the speed of moult, which varies as a function of growth  
46 rate moult and intensity through time; 4) moult duration, which depends on moult speed and  
47 plumage volume and correlates to body size (Rohwer *et al* 2009), and can be measured when  
48 the moult process is completed.

49         Feathers are replaced following a sequence that can be highly conserved within some  
50 tracts (e.g. primaries) although it shows a large variation among tracts (Guallar *et al* 2009,  
51 Jenni *et al* 2020a). Moult sequence affects plumage performance during moult and the set of  
52 feathers replaced in partial moults (Echeverry-Galvis & Hau 2013, Guallar & Jovani 2020).

53         The moult output can be described and quantified in terms of several components:  
54 extent, which measures the investment in the moult process and is positively correlated to  
55 moult duration (e.g. Newton 1966); the set of feathers that an individual bird replaces in a  
56 given moult episode (Guallar & Jovani 2020); and feather quality, a broad term that refers to  
57 the feather's physical properties, which correlates to function, habitat, and physical condition  
58 (Pap *et al* 2008, 2013, 2015, 2017; Griggio *et al* 2009, Ross *et al* 2015).

59         The wing-feather moult is mainly described by focusing on the remiges and greater  
60 coverts. Nevertheless, the moult of the other wing feathers may potentially provide

61 information on relevant aspects of plumage that are influenced by intrinsic and extrinsic  
62 factors, and on strategies employed to reduce function loss and maladaptation. Yet, moult  
63 descriptions of the marginal coverts (also named lesser coverts, although this name should not  
64 be applied to passerines according to Winkler & Jenni 1996) are generally neglected, and even  
65 comprehensive moult accounts do not provide much information on these coverts (e.g. Zeidler  
66 1966), probably due to their small size and large number. Although most of the variables that  
67 describe the active moult of these feathers are still poorly documented, descriptions of  
68 incomplete marginal-covert moults are often provided (Jenni & Winkler 2020a, 2020b). For  
69 example, Jenni & Winkler (2020b) comment the extent of marginal coverts in partial moults,  
70 although their description is limited to rough estimates in terms of both the percentage of the  
71 total marginal coverts and their spatial distribution (i.e. whether or not the new feathers are  
72 proximal, distal, anterior, or posterior; Guallar *et al* 2014).

73 To fill this gap in our knowledge, we quantified the moult of marginal coverts in an  
74 urban House Sparrow *Passer domesticus* population. We selected this sparrow as a study  
75 species because it is abundant and its marginal coverts are easy to describe. House Sparrows  
76 have 50–55 marginal coverts arranged as follows: one row of minute feathers outlining the  
77 leading edge of the wing from the scapulars to the alula, and five rows of feathers increasing in  
78 size towards the median coverts (Figure 1). Specifically, here we document eight moult  
79 components grouped in three sections: i) time-related components, which include timing,  
80 growth rate (only of the largest marginal covert), intensity, speed, and duration (both of the  
81 complete group of coverts and of the largest marginal covert); ii) moult sequence in the  
82 marginal coverts and relative to body and wing feathers, and iii) output components, which  
83 include extent, size, and barb density.

84

85 **Methods**

86 As part of the PASSERCAT project targeting House Sparrow survival (Covas *et al* 2017), we set  
87 up two study sites in Parc de la Ciutadella, a 17.5-ha park in Barcelona (41°23'21 N, 2°11'6 E)  
88 that is home to the city's zoo. Both sites had six funnel traps with freely accessible peanut  
89 feeders and *ad libitum* feeding for small-size birds. During eight weeks, from mid-August to  
90 early October (i.e. coinciding with the moulting season of the local House Sparrow population),  
91 the traps were deployed one morning per site per week, approximately from 08.00 until 14.00  
92 h. Traps were checked hourly and captured birds were ringed and processed following  
93 PASSERCAT protocols (Covas *et al* 2017). A winter field season also spanning eight weeks, from  
94 mid-January to mid-March, followed the same protocol. We took the following information  
95 from the data recorded in the field: moult, date, sex, and age. Age was determined by the  
96 presence or absence of juvenile feathers, which were identifiable until the moult had finished.  
97 Once moult was finished, we were still able to age most birds by checking the degree of skull  
98 ossification (Winkler 1979).

99 We completed 181 active-moult cards (26 adults and 155 first-year birds) from our  
100 urban population in Barcelona during the summer seasons in the years 2018–2021 (all data  
101 taken by the same observer, SG). For comparative purposes, we also analysed an independent  
102 dataset (N = 999, 368 adults and 631 juveniles) covering the onset of House Sparrow moult in  
103 2018–2021. This dataset, which provides information regarding the presence/absence of  
104 moult during the period in which the onset of House Sparrow moult occurs, includes  
105 information from ringing stations located in non-urban areas throughout Catalonia gathered  
106 by the Catalan Ornithological Institute (ICO 2021).

107 Specific data for growth rate, intensity, speed, sequence, size, and barb density were  
108 only collected in 2021 (N = 33 unless stated otherwise). We provide mean and standard  
109 deviations throughout unless stated otherwise. Analyses were performed using R v4.1.2 (R  
110 Core Team 2021).

111 Renewed marginal coverts were scored as a percentage of the total number of marginal  
112 coverts. On the other hand, the percentage of growing marginal coverts was down scored to  
113 half since the moult progress of each of these growing feathers is considered to average  
114 halfway between the old and the new feathers. As an example, 40% fully grown marginal  
115 coverts plus 10% growing marginal coverts was scored as  $40\% + 10\%/2 = 45\%$ .

### 116 *Time-related components*

117 The mean  $\pm$  standard error of moult start- and end-dates for the marginal coverts of our House  
118 Sparrow population and for the start-date of the general moult of the non-urban dataset were  
119 estimated using generalised linear models with a binomial distribution and a probit link  
120 function (Rothery & Newton 2002): moult presence/absence  $\sim$  date + sex + age. We built four  
121 models, one for each possible combination between the date and the other two covariates,  
122 and then selected the one with the lowest AIC for both the start- and end-date (Burnham &  
123 Anderson 2002).

124 To estimate feather growth rate, we measured the width of daily growth bars of the  
125 plucked marginal coverts (i.e. one dark bar plus one consecutive pale bar; Grubb 2006).  
126 Specifically, we selected the innermost marginal covert plucked from the trailing-edge row,  
127 which is the largest marginal covert. Measurements were taken using image-manipulation  
128 software from photographs of the feathers placed on a ruler (GIMP 1995-2020; Figure 2A).

129 Instantaneous moult intensity was estimated by counting the number of growing  
130 marginal coverts, whose pins were exposed by soaking the marginal coverts in 96° ethanol  
131 (Figure 2B). We calculated instantaneous moult speed from the score increase between  
132 capture and recapture dates. To this end, we only used individuals that were actively moulting  
133 their marginal coverts since it is impossible to determine the lag occurring before or after  
134 active moult. We also calculated the population's mean speed of the general moult progress  
135 by dividing 100% by the estimate of mean moult duration.

136 Mean moult duration of the marginal coverts for the population was obtained by  
137 subtracting the mean start-date from the mean end-date; while its pooled standard error was  
138 averaged from the start- and end-date estimates (pooled error of two samples of equal size).  
139 The duration of individual feather growth was calculated as the feather length (vane and  
140 calamus) divided by its growth rate.

#### 141 ***Sequence***

142 We photographed the whole group of marginal coverts to show their progress and the position  
143 of growing feathers within the group. To track the moult sequence within the marginal coverts,  
144 we sketched the area occupied by old, growing, and new feathers on 67 active-moult cards.  
145 We also established the moult sequence relative to other feather groups by comparing the  
146 start of the marginal-covert moult with wing (primaries, secondaries, tertials, greater coverts,  
147 and median coverts), tail (rectrices), and body feathers.

#### 148 ***Output components***

149 The moult extent was quantified as the number of moulted marginal coverts in birds in the  
150 winter dataset. To document feather length, calamus width (a proxy of follicle size) and barb  
151 density of marginal coverts, we followed the procedure above described for measuring growth  
152 rate. We weighed the mass of the largest marginal covert to the nearest 0.1 mg using a  
153 Sartorius AG ED 124S scale. In addition, we presented length and mass of primary P7 and  
154 rectrix R5, which are the two feathers most frequently used in studies that measure growth  
155 rate and barb density in the House Sparrow (e.g. Vangestel *et al* 2010, Pap *et al* 2008, 2013).  
156 We measured the lengths of 10 consecutive barbs along the central part of the rachis to  
157 quantify barb density.

158 In order to show the relationship between size and marginal-covert moult, we  
159 regressed barb density and growth rate on our two proxies of feather size (i.e. length and

160 mass) using ordinary least squares. We used this same method to analyse the relationship  
161 between feather size and our proxy of follicle size (i.e. calamus width).

162

## 163 **Results**

### 164 ***Time-related components***

165 Timing. The binomial models to estimate start- and end-dates which had a best fit (i.e.  
166 minimum AIC) retained date and age as independent variables, discarding sex for both the  
167 Barcelona and the non-urban datasets (Table 1). The Barcelona House Sparrow population  
168 moulted its marginal coverts in July–October. Four birds finished moulting their marginal  
169 coverts as early as 17 August, while three others – including one that had a score of only 10%  
170 on 8 October – were still growing them in early October (all seven were first-year birds; Figure  
171 2C). Start- and end-dates for the adult population were estimated on 29 July  $\pm$  18.58 days and  
172 29 August  $\pm$  21.03 days, respectively, with hatch-year birds starting 13.63  $\pm$  19.31 days later  
173 and finishing 13.51  $\pm$  22.26 later (Table 1A). Adults in the non-urban dataset had a later  
174 general moult onset, estimated on 10 August  $\pm$  21.55 days, with hatch-year birds starting 9 July  
175  $\pm$  21.84 days (Table B).

176 Growth rate. The growth rate of the largest marginal covert was estimated at 1.10  $\pm$   
177 0.12 mm/day (N = 30). We did not find significant differences between sexes (t test: t = 0.016,  
178 P = 0.988).

179 Intensity. The instantaneous moult intensity as the moult of the marginal coverts  
180 progresses describes an M-shape curve. The second peak is caused by the simultaneous  
181 growth of feathers on the leading and trailing edges (small and large, respectively; Figures 1, 3,  
182 and 4).



183            Speed. The instantaneous speed calculated from recaptures (N = 6) was  $5.06 \pm 2.48$   
184   %/day, while the mean speed of the moult progress for the population was  $100/31.91 = 3.13$   
185   %/day.

186            Duration. The duration of the moult of the marginal coverts in our population was  
187   estimated at  $31.91 \pm 19.80$  days. The growth duration of the largest marginal covert was  $14.10$   
188    $\pm 7.01$  days.

### 189   **Sequence**

190   House sparrows start moulting a few marginal coverts near the scapulars. Shortly afterwards,  
191   the pins spread towards the carpal joint. When these feathers are fully grown, the moult  
192   spreads simultaneously toward the leading and trailing edges. The final marginal coverts to  
193   grow are those that cover the elbow and the leading edge (Figure 4).

194            Marginal coverts start growing shortly after the primaries begin to grow. Although they  
195   can start growing before primary P2 (two out of 33 cases) or as late as primary P6 (three out of  
196   33 cases), in most cases (28 out of 33) they start between P2 and P6. In six out of 33 cases, the  
197   moult of the marginal coverts started after the onset of moult in the greater coverts (the other  
198   27 started before the onset of greater covert moult), and in five cases after the onset of the  
199   median-covert moult and tertial moult (remaining cases started before). In four out of 33  
200   cases, the marginal-covert moult started after the onset of moult in secondaries, and twice  
201   after that of rectrices (remaining cases started before). Finally, out of 17 cases, the moult of  
202   the marginal coverts in five cases started before the onset of moult of body feathers  
203   (remaining cases started while body moult was underway).

### 204   **Output components**

205   Extent. House Sparrow moults once a year, and its moult is complete both in adults and in  
206   hatch-year birds (Zeidler 1966, Pyle 1997; but see Guallar & Quesada 2021). Very infrequently,

207 House Sparrows retain a remex (one out of 127 individuals captured in winter). We only  
208 detected one bird that had retained one juvenile marginal covert on the leading edge (it had  
209 pale brown centre and whitish margin, contrasting with the remaining ones which were black  
210 and white). Therefore, the extent of the marginal coverts in our winter sample was complete  
211 in 99.21% cases (N = 140).

212 Feather size. The largest marginal covert in the Barcelona population averaged more  
213 than 5 times shorter and more than 30 times lighter than both primary P7 and rectrix R5 (Table  
214 2), while its calamus averaged 5.2 and 3.4 times narrower, respectively (Table 2). Size of the  
215 largest marginal covert increased with calamus width, although the effect was not significant  
216 (Figure 5A). We found no sex differences in length, mass, or calamus width (t-test: P = 0.404, P  
217 = 0.485, P = 0.091, respectively). Barb density tended to decrease with feather length although  
218 the effect was not significant (Figure 5B). Growth rate increased significantly with both feather  
219 length and mass (Figure 5C).

220 Barb density. The barb density of the largest marginal covert in the Barcelona  
221 population was  $3.23 \pm 0.44$  barbs/mm. Females averaged higher barb density than males  
222 although differences were not significant (t test: t = 0.459, P = 0.653).

223

## 224 **Discussion**

### 225 ***Time-related components***

226 Although we cannot directly compare the start date of the general moult of the non-urban  
227 dataset and the start date of the marginal coverts of the Barcelona population, it is very  
228 striking that moult onset of hatch-year birds in the Barcelona population is delayed 13 days in  
229 relation to that of adults moult, whereas in the non-urban dataset moult onset is advanced 31  
230 days. Age-differences in marginal-covert moult timing could be explained by a protracted

231 breeding season in our Barcelona population, which may not only start earlier than in non-  
232 urban populations but also end later as suggested by the presence of hatch-year birds in the  
233 early stages of moult in October (Figure 2C; Chamberlain *et al* 2009, Fudickar *et al* 2017).

234 The growth rate by length of marginal coverts averages about three times lower than  
235 that observed for the primary P7 in the House Sparrow (3.6 mm/day, approximately; Pap *et al*  
236 2008). These results are consistent with our data: the growth rate extrapolated from the linear  
237 regression of marginal covert length on growth rate averages 3.75 mm/day for primary P7, 3.4  
238 times higher than the mean growth rate of the largest marginal covert (Figure 5C). Similarly,  
239 growth rate by length of rectrix R5 extrapolated from the linear regression of marginal covert  
240 length on growth rate averages 3.65 mm/day (Table 2), fairly close to the mean growth rate by  
241 length measured for 12 rural populations in Belgium (3.36 mm/day; Vangestel *et al* 2010). The  
242 great differences between the growth rate by length between largest marginal covert and  
243 rectrix R5 and primary P7 are likely to be related to differences in follicle size between these  
244 feathers and marginal coverts: as the follicle becomes smaller, the feather growth rate drops  
245 (Figure 5; Jenni *et al* 2020).

246 The moult intensity of marginal coverts is approximately quadratic in form albeit with an  
247 early peak (left skewness in Figure 3), coinciding with the second moult-sequence stage (Figure  
248 4). This rapid replacement of the central feather rows scarcely overlaps with the replacement  
249 of the leading and trailing feather rows, which begins after most of the central ones are fully  
250 grown. This strategy could help reduce skin exposure and general functional loss such as  
251 thermal isolation and protection from mechanical abrasion (Bonser 1995, Wolf & Walsberg  
252 2000), which can be important in Mediterranean areas. The aerodynamic camber may be  
253 altered during the moult of marginal coverts (although camber may not play a role as  
254 important in the House Sparrow as in species that spend more time flying; Shyy *et al* 2013).

255 Discrepancies with the instantaneous and mean moult speed of marginal coverts are probably  
256 due to the fact that their moult intensity varies as moult progresses.

257 Interestingly, the moult duration of marginal coverts in our House Sparrow population  
258 took a very similar time to the duration in the Azure-winged Magpie *Cyanopica cooki* (as far as  
259 we know, this information is not available for any other species), a species that is about four  
260 times heavier (De la Cruz *et al* 1992, Dunning 2007). On the other hand, the long growth  
261 period of individual marginal coverts suggests that the allometric effect between moult  
262 duration and bird species size also occurs at individual level since feather size negatively  
263 correlates with feather growth rate (Figure 5; Jenni *et al* 2020). We only measured the largest  
264 marginal covert, so that variation between marginal coverts (which show notable differences  
265 in size; Figure 1) remains unknown.

#### 266 **Sequence**

267 Sequence of replacement within the marginal coverts in the House Sparrow is ordered and  
268 consistent in our dataset. However, our results slightly differed from the moult description  
269 given by Zeidler (1966: p 134), who stated that the marginal-covert in the House Sparrow  
270 starts at the front and proceeds towards the rear. On the other hand, our results agreed with  
271 those described for the complete moult in the Eurasian Bullfinch *Pyrrhula pyrrhula*, likely  
272 because the marginal-covert moult was treated in more detail in this species (Newton 1966).  
273 The biological meaning of the sequence of replacement within the marginal coverts is  
274 unknown, although it might reduce functional loss in comparison with other possible  
275 sequences.

276 While moult in the House Sparrow starts by shedding the innermost primary in circa  
277 100% cases (Zeidler 1966), the start of marginal-covert moult in relation to other feather tracts  
278 is quite variable. It tends to occur after body feathers start moulting, as documented habitually  
279 in other species (Dwight 1900, De la Cruz *et al* 1992). However, around one third of the birds in

280 our sample started moulting their marginal coverts before their body feathers, thereby  
281 matching the descriptions by Zeidler (1966) and the sequence of the complete postnuptial  
282 moult in the Eurasian Bullfinch (Newton 1966). Also, the start of marginal-covert moult in  
283 relation to the primaries shows more variability than that documented by Zeidler (1966), who  
284 merely stated that it occurs after primary P2 is shed. Variability in the relative start of moult  
285 among feather tracts is the norm (Winkler et al 1988, Guallar *et al* 2009) although its biological  
286 implications remain largely speculative (Jenni & Winkler 2020b), and in the case of the  
287 marginal coverts it could well be nonadaptive.

### 288 ***Output components***

289 Complete postjuvenile moult is more prevalent in passerine species such as the House Sparrow  
290 that have clear sexual dichromatism and no delayed plumage maturation (Delhey *et al* 2020).  
291 The fact that only very rarely are any of the approximately 50 marginal coverts retained  
292 suggests that very tight moult control is exercised. Moult studies in passerine species  
293 undergoing moult episodes with retention of marginal coverts could benefit from descriptions  
294 of marginal-covert moult (e.g. Eurasian Reed Warbler *Acrocephalus scirpaceus* and some  
295 *Empidonax* flycatchers; Leisler & Schulze-Hagen 2011, Carnes *et al* 2021).

296 We found that the barb density of the largest marginal covert was approximately 1.6  
297 times higher than that reported for primary P7 in a farmland population of House Sparrow in  
298 Romania (4.9 barbs/mm, approximately; Pap *et al* 2013). These results are consistent with our  
299 data: the barb density extrapolated from the linear regression of marginal-covert mass on barb  
300 density averages 4.88 barbs/mm for primary P7, 1.55 times higher than the mean barb density  
301 of the largest marginal covert (Figure 5B). We also found a great deal of barb-density variation  
302 for the largest marginal covert in our dataset, which could be explained by factors such as sex  
303 and physical condition. Indeed, males of the European Greenfinch *Chloris chloris* have rectrices  
304 of better quality than females (Minias *et al* 2015), and barb densities are positively associated

305 with feather quality via physical condition (e.g. severe parasite infestation correlates  
306 negatively to barb density; Pap *et al* 2013).

### 307 **Concluding remarks**

308 We have provided detailed information on the moult of the marginal coverts in a House  
309 Sparrow population in the city of Barcelona using eight components that encompass the moult  
310 process and its output. Comparison of our results with those of flight feathers (e.g. primaries  
311 and rectrices) may help acquire a better understanding of how feather function and structural  
312 properties are linked and how extrinsic and intrinsic factors shape them. Indeed, collation of  
313 our Barcelona population and non-urban populations reveals a correlation between habitat  
314 and both moult timing and growth rate (Vangestel *et al* 2010, Pap *et al* 2013). In addition, we  
315 found no sex effects on moult timing, growth rate, feather size, or barb density. This is  
316 surprising since marginal coverts show a high degree of sexual dichromatism. On the other  
317 hand, we found that age influences moult timing. Unfortunately, low sample size lowered the  
318 robustness of our results and impeded testing age differences in growth rate, feather size, or  
319 barb density.

320 Although function and size are closely related, feather types of similar size may differ in  
321 their moult components. Future allometric studies should compare moult components among  
322 feather types to shed light on the biological meaning of possible deviations, as those already  
323 found between outer and inner primaries (Dawson 2005).

324

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331

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440 **Table 1.** (A) Summary of the binomial models selected to estimate start- and end-dates for the  
 441 marginal-covert moult in the House Sparrows captured in Parc de la Ciutadella, Barcelona (N =  
 442 181). (B) Summary of the binomial model selected to estimate start date of general moult in  
 443 the non-urban dataset (N = 999), during the study period 2018-2021. Model selection was  
 444 carried out for all combinations of age, sex, and Julian date as covariates. The untransformed  
 445 results of the binomial models with the lowest AIC are given. Significant effects are shown in  
 446 bold face.

447

	Estimate	Std error	p-value
A) Start (AIC = 101.65)			
Intercept	0.153	0.645	0.813
Date	0.054	0.015	<b>&lt;0.001</b>
Age (juveniles)	-0.734	0.569	0.197
End (AIC = 201.09)			
Intercept	-1.383	0.406	<b>&lt; 0.001</b>
Date	0.048	0.008	<b>&lt; 0.001</b>
Age (juveniles)	-0.642	0.318	<b>0.044</b>
B) Start (AIC= 901.22)			
Intercept	-10.276	0.730	<b>&lt; 0.001</b>
Date	0.046	0.004	<b>&lt;0.001</b>
Age (juveniles)	1.483	0.122	<b>&lt;0.001</b>

448

449

450 **Table 2.** Mean  $\pm$  standard of two feather-size proxies and a proxy of feather-follicle size  
451 (calamus width) for the largest marginal covert, primary P7, and rectrix R5 in the House  
452 Sparrow population from the city of Barcelona.

	N	Length (mm)	Mass (mg)	Calamus width (mm)
Marginal covert	33	11.73 $\pm$ 1.24	0.35 $\pm$ 0.09	0.19 $\pm$ 0.06
Primary P7	4	64.56 $\pm$ 2.50	13.66 $\pm$ 1.71	0.98 $\pm$ 0.04
Rectrix R5	4	61.97 $\pm$ 2.76	11.40 $\pm$ 0.98	0.64 $\pm$ 0.13

453

454

455 **Figure 1.** Upper marginal coverts (yellow dots) cover the arm and hand of the bird's wing. We  
456 took a restricted approach in this study and only considered the marginal coverts covering the  
457 arm, from the scapular to the carpal-alular regions and from the leading edge to the row of  
458 median coverts. AF: alula feathers, CC: carpal covert, MC: median coverts, SC: scapulars.

459 **Figure 2. A)** The growth bars of marginal coverts are very tenuous, of which eight can be seen  
460 in the photograph. **B)** Growing marginal coverts, of which nine can be seen in the photograph.  
461 **C)** Timing of the marginal-covert moult during the study period 2018–2021 (N = 181). Data  
462 pooled for the intervals indicated along the X-axis. In parenthesis, the percentage of  
463 individuals moulting marginal coverts within each time interval. The curve fits a LOESS  
464 regression using all points to reduce wiggleness (standard errors not shown).

465 **Figure 3.** Moult intensity of marginal coverts (scored as number of growing feathers) as a  
466 function of moult progress within this group of feathers (N = 22). The curve depicts a LOESS  
467 regression with  $\alpha = 0.65$  to emphasise local effects. Grey area depicts standard errors.

468 **Figure 4.** Moult progress of marginal coverts; old feathers are not depicted, only growing (as  
469 pins) and full-grown new ones. Moult of marginal coverts begins near the body and spreads  
470 first towards the carpal joint and then expands simultaneously toward the trailing and the  
471 leading edges. The last marginal coverts to be replaced are those covering the elbow. Growing  
472 feathers depicted as pins for ease of interpretation, although they can be at any growth stage.

473 **Figure 5.** Coefficient estimates,  $R^2$  and p-value for the regression of marginal-covert size on (A)  
474 calamus width (mass = 224.97,  $R^2 = 0.079$ ,  $P = 0.056$ ; length = 0.009;  $R^2 = 0.006$ ,  $P = 0.277$ ), (B)  
475 barb density (mass = 129.81,  $R^2 = -0.029$ ,  $P = 0.837$ ; length = -0.067;  $R^2 = 0.039$ ,  $P = 0.131$ ), and  
476 (C) growth rate (mass = 695.4,  $R^2 = 0.272$ ,  $P = 0.001$ ; length = 0.051;  $R^2 = 0.259$ ,  $P < 0.001$ ).

477

FIG 1

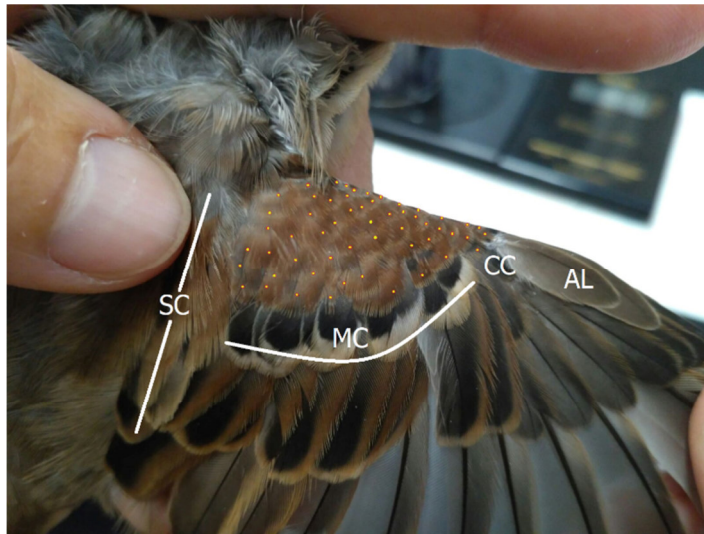
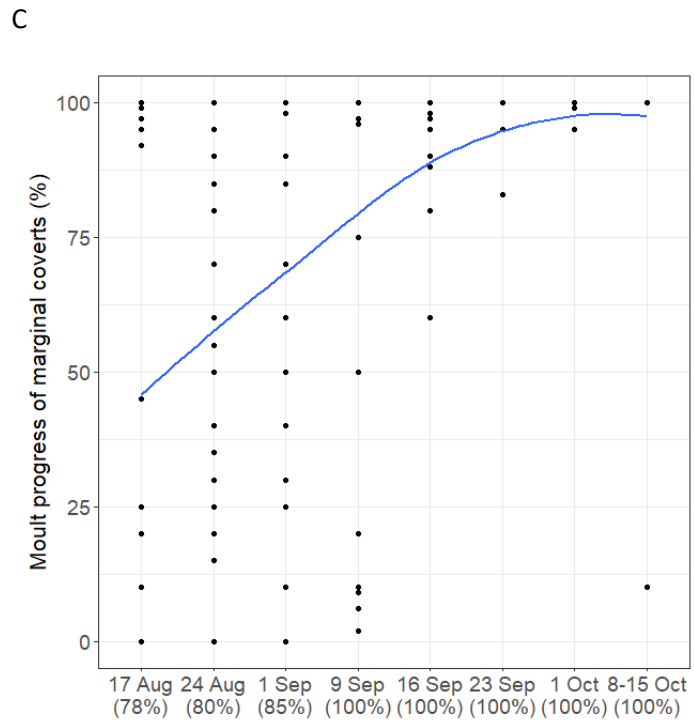
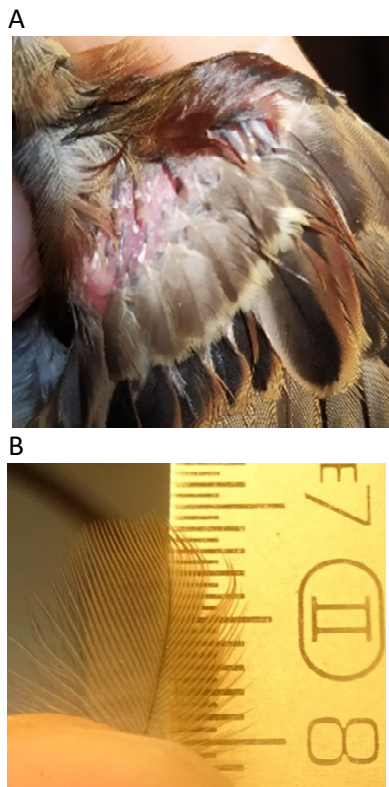
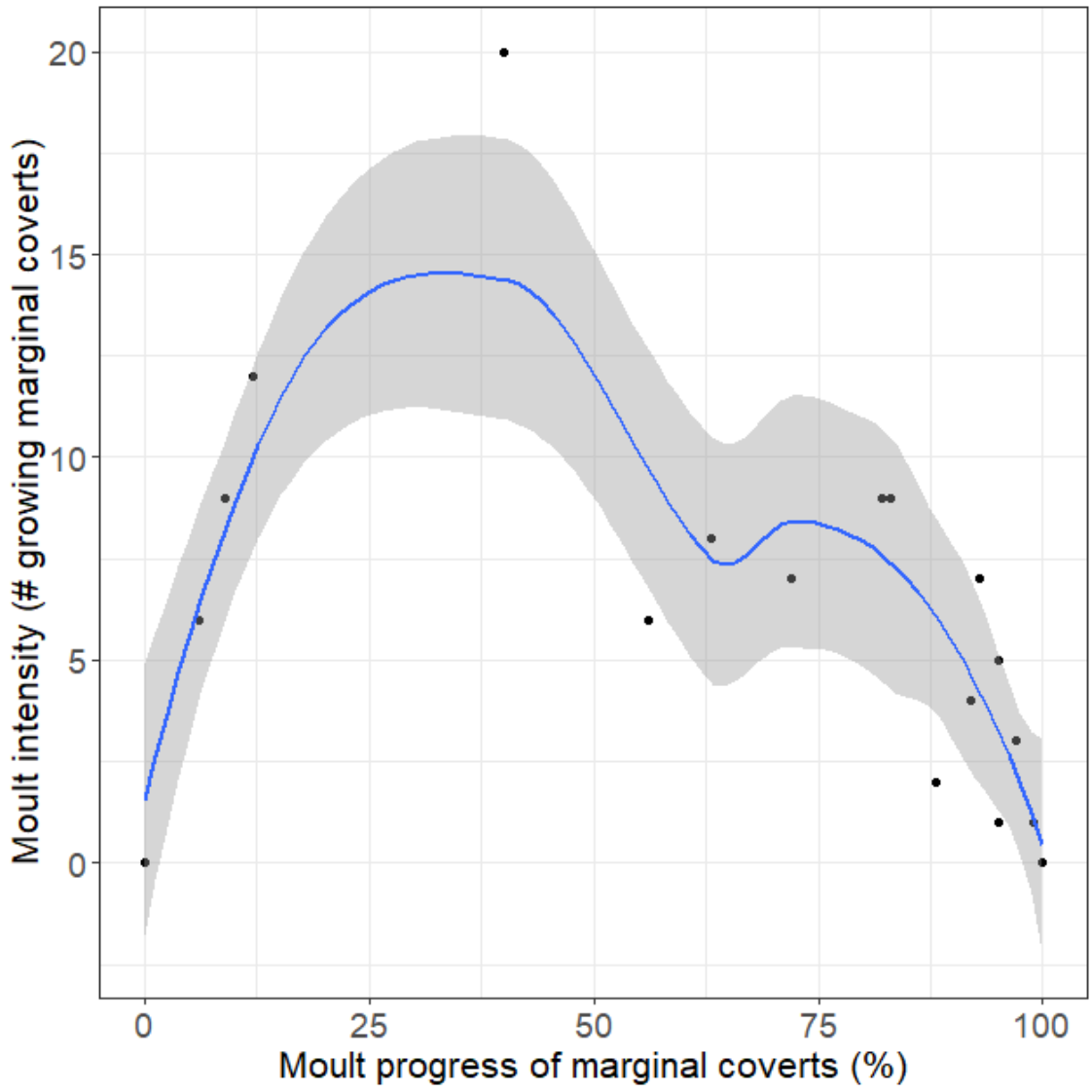
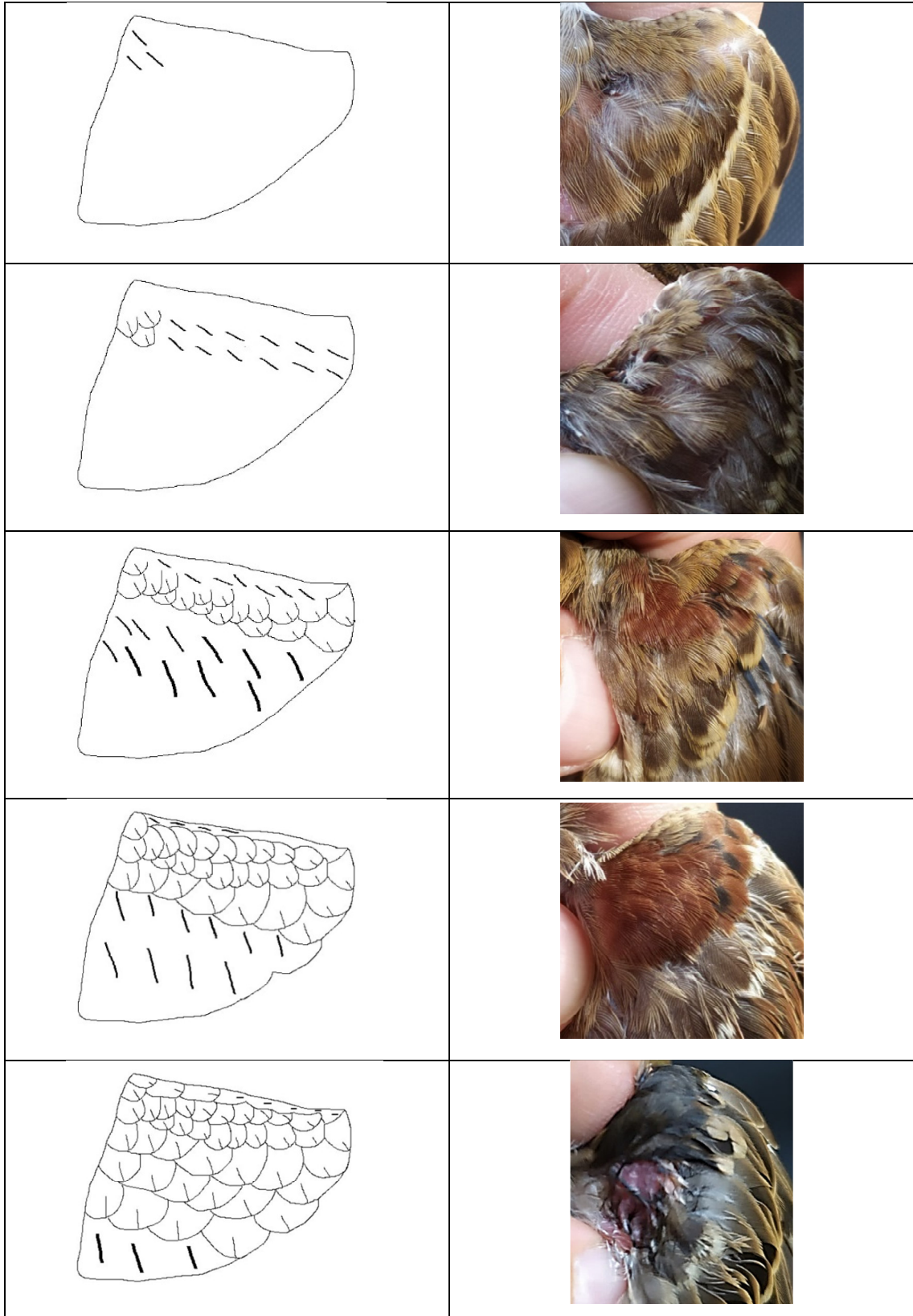


FIG 2





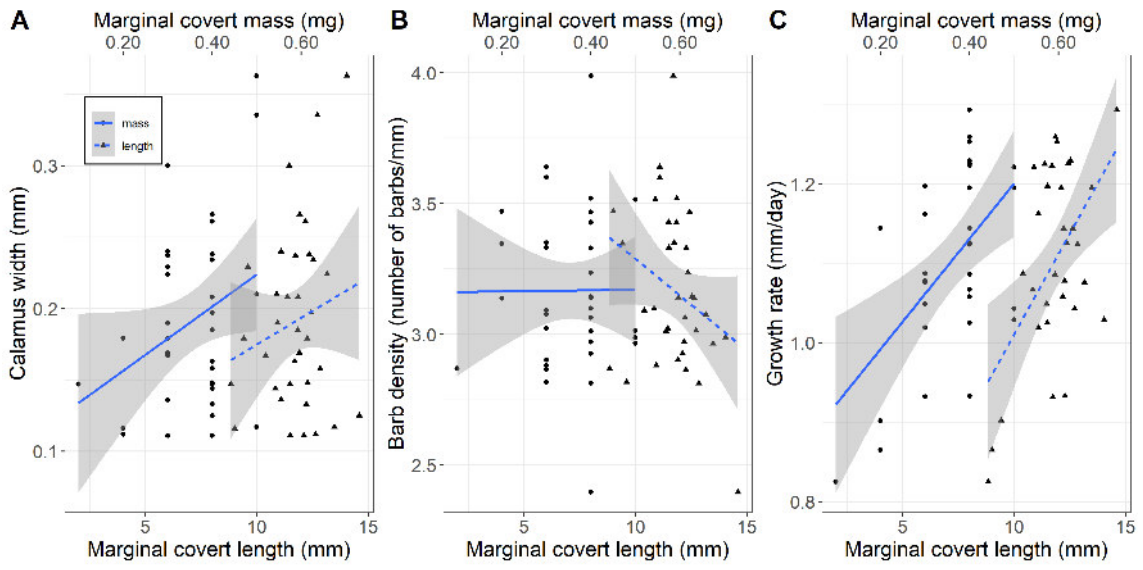




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FIG 5

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