

1 **A timeline for the urbanization of wild birds: the case of the lesser kestrel *Falco naumanni***

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22

23 **Abstract**

24

25 The Lesser kestrel (*Falco naumanni*) evolved as a separate species in the Old-World
26 kestrel radiation starting in the late Miocene. Given that the first cities were erected in the
27 Holocene, this urban colonial raptor has only become a major town dweller recently in its
28 evolutionary history. Today, more than 95% of lesser kestrel colonies in Spain and other

29 Mediterranean countries are on buildings, and the remaining few are on rocky outcrops, that
30 may have been the original nesting substrate for this cavity-nesting bird. Lesser kestrel fossils
31 are well represented in cave sites, and their paleontological distribution, spanning from the
32 Early Paleolithic to the Epipaleolithic, agrees well with its current breeding distribution.
33 According to classical sources, such as the works of Columella and Pliny the Elder, and the
34 presence of a skeletal remain in a Roman villa near Madrid, lesser kestrels may have nested in
35 buildings and in urban settings for at least 2000-2500 years. However, there are no surviving
36 colonies in structures older than 1400 years in Andalusia, nor in Spain. For a sample of 349
37 colonies on ancient buildings, a majority of the structures had been erected in the 15th and 16th
38 centuries, this putting a time limit of 400-500 years to the existence of those seemingly
39 immemorial colonies. For specific towns and buildings, written references for the presence of
40 lesser kestrel colonies do not go back more than two centuries. In fact, the Cathedral of Sevilla
41 may be the structure with the longest continuous occupation by lesser kestrels recorded up to
42 present time, from at least Cook (1834) to year 2020 breeding season. Lesser kestrels were
43 possibly too common in human settlements in the past as to be noted as special. This may
44 explain the scarcity of references to the species until the 19th century. In any case, the same
45 lack of information affects the other major Eurasian urban birds, as no timeline exist for the
46 urbanization process of any other bird species. We propose that lesser kestrels became urban
47 breeders when both adequate cavities in buildings and cereal fields, where they capture their
48 invertebrate prey, became available in their breeding range, several millennia ago. However,
49 urban colonies, in contrast with the ones on stable geological substrates, have been forced to
50 move from building to building when older ones became ruinous or were rebuilt, but new
51 structures with suitable cavities became available throughout History.

52

53

54 Keywords: urban wildlife, Falconidae, cavity nester, coloniality, human habitat, zooarchaeology

55

56 **Introduction**

57

58 The cohabitation of animal species with humans in urban environments has only been
59 possible since the inception of permanent settlements in the Holocene, less than 12,000 years
60 BP. Nonetheless, some urban species may have a much longer and previous association to
61 human dwellings along the Pleistocene, as cave species shared breeding, roosting or even

62 foraging habitat with cave people (Larson et al. 2004). One well documented case is the rock
63 dove *Columba livia* (Blasco et al. 2014). This species is the most cosmopolitan urban bird
64 species nowadays (Aronson et al. 2014). Rock doves were already breeding in caves in
65 prehistory, where they were consumed by Neanderthal peoples and, after their extinction, by
66 modern humans in the same locations (Blasco et al. 2014).

67 The relationship between cave people and the set of cave-dwelling bird species was
68 generally one of predation for consumption, but some species were also coveted for the
69 ornamental value of their feathers (Peresani et al., 2011, Finlayson et al. 2012). Raptors figured
70 prominently among these species with a symbolic value (Negro 2018), including large species
71 such as bearded vultures *Gypaetus barbatus*, but also the small kestrels, as with the red-footed
72 falcon *Falco vespertinus* (Peresani et al. 2011).

73 Urbanization has been an uneven process at a planetary scale (Stephens et al. 2019). In
74 the New World, where humans arrived late –about 18,000-30,000 years ago (Ardelean et al.
75 2020)-, corporate architecture and urban settlement did not start until about 4.000 years BP at
76 places like Caral, in Peru (Shady Solis et al. 2001). Rather late compared to 10.000 years BP
77 estimated for cities like Jericho in the Old World. However, North America was mostly devoid
78 of permanent cities until the arrival of Europeans, and the oldest continuously occupied city in
79 the United States, St. Augustine, was founded by Spaniards in 1565 (Ring et al. 2013). In North
80 America, genuine urban birds, considering as such those nesting normally on buildings (Erz
81 1966), all have a post-colonization European origin, and were thus transported: house
82 sparrows were first released in Brooklyn, NY, in 1851 (Moulton et al. 2010); the starling was
83 introduced in Central Park, NY, in 1890 (Thacher Cooke 1928), and the rock dove was
84 introduced in the early 1700's (Schorger 1952). The peregrine falcon, with a large urban
85 population in North American cities today, was in fact introduced in urban environments in the
86 second half of the 20th century (Gahbauer et al. 2015).

87

88 Species breeding on buildings are few, they tend to be colonial, and all have the ability
89 of “cliff-breeding” (Erz 1966, Larson et al. 2004). They include, apart from the cosmopolitan
90 house sparrows, starlings and rock doves (Aronson et al. 2014), the white stork *Ciconia ciconia*
91 and the lesser kestrel *Falco naumanni* in Mediterranean countries. Other synanthropic avian
92 species that may have an ancient association with human buildings are the jackdaw *Corvus*
93 *monedula*, house martin *Delichon urbicum*, the barn swallow *Hirundo rustica*, and different
94 swift species (*Apus spp.*). Some owls may also be found in buildings. The barn owl *Tyto alba*
95 has become the quintessential town owl around the world, although, quite paradoxically,

96 recent population declines have been attributed to increased urbanization (Hindmarch et al.
97 2017).

98

99 The process of urbanization for certain bird species that have established urban
100 populations in cities in the 20th century has been relatively well documented (see Chace and
101 Walsh 2006 for a review). However, for the seemingly ancient urban bird colonizers of
102 European cities mentioned above, little is known of how and when they became urban birds.
103 Historical accounts before the 19th century are scarce. Remains in archeological sites of the
104 classical period (i.e., Roman and later) are scarce (Kroll 2012, García Petit 2017). The few
105 attempts to model the urbanization process of bird species have resulted very simplistic:
106 current paradigm is that hole nesting species became urban as soon as they found cavities in
107 buildings and there was food for them in the city itself or in the surroundings (e.g., Summers-
108 Smith 1988, pp 281-282, for the house sparrow). But it is unknown whether urban colonies
109 stayed continuously in any given location or suffered extinctions and recolonizations (Levins
110 1970), as would be expected of metapopulations (Keymer et al. 2000, Serrano and Tella 2003).

111

112 The picture is indeed complex, as all species involved have kept out-of-the-city
113 populations with which there has been genetic admixture (e.g., Alcaide et al. 2009 for lesser
114 kestrels), so that no clear morphological adaptations (McDonnell and Hahs 2015) setting apart
115 urban and rural breeding populations have yet been detected (but see Mueller et al. 2018 and
116 Mueller et al. 2020 for genetic signatures of urbanization, and Watson et al. 2017, for
117 physiological responses). Even though urbanization is an ever-growing process, and although
118 some urban breeders keep the largest avian populations worldwide (house sparrows, starlings
119 and rock doves number hundreds of millions of individuals each, Aronson et al. 2014), others
120 have declined sharply in the 20th century (e.g., white stork and lesser kestrel), with one urban
121 breeder, the Bald Ibis *Geronticus eremita*, getting fully extinct in Europe and on the verge of
122 extinction globally (Del Hoyo et al. 1992). Recently, it has been suggested that cities may
123 become ecological traps for birds, as their breeding success is often lower than in rural areas
124 (Pollock et al. 2017). Assessing whether some species have bred for centuries or even millennia
125 in urban environments may thus shed light on particular adaptations for long-term
126 cohabitation with humans (see, e.g., Erz, 1966, McDonnell and Hahs 2015, Møller and Xia
127 2020).

128 The lesser kestrel *Falco naumanni* is a colonial small falcon, with fully or partially
129 migratory populations in Eurasia (Negro et al. 1991). About 95% of breeding couples in the
130 Iberian peninsula (Iberia onwards), the largest European population (González and Merino
131 1990), nest on buildings, and a majority of them do so inside towns or cities. Lesser kestrels are
132 also urban in all countries in the western end of its distribution, currently having major
133 breeding populations in Spain, Italy, Greece, Turkey, and Morocco (Negro 1997). This makes
134 the lesser kestrel the most urban of all birds of prey in the Western Palearctic, and possibly in
135 the world. Notwithstanding the current dependence of the species on human dwellings, we do
136 not know when or how the urban habit emerged for this species. In fact, eastern populations
137 in the Asian steppes and northern China have never been attached to human buildings, and
138 have used (Brehm 1858) and still use rocky outcrops and sandy river banks instead (Parr et al.
139 2000).

140 We have used different data types, including paleontological records, ancient accounts
141 and scientific literature from the 19th, as well as contemporary colony site data, to build a
142 plausible scenario of how and when lesser kestrels became major urban breeders in the
143 western portion of its distribution range. Our aim has been to elaborate a historical timeline
144 for the urbanization process of the lesser kestrel, taking Andalusia, a stronghold for the species
145 in Iberia with an intensively monitored population, as the main study area for our analysis.

146

147 **Material and Methods**

148

149 **Study species: the lesser kestrel**

150

151 The kestrels (17 species within the genus *Falco*) commenced to radiate in the late
152 Miocene, within the last 8 million years, coincidental with the expansion of open habitats
153 (Fuchs et al. 2015). Lesser kestrels are the sister taxon of 9 other extant kestrels. All together,
154 these 10 species conform the Old World kestrel group, that evolved from a common ancestor
155 about 4 million years ago (Fuchs et al. 2015). In fact, fossil data agree well with DNA sequence
156 inferences: an extinct large kestrel species, *Falco hezhengensis*, that just predated the above
157 mentioned radiation, has been found in the Late Miocene (about 6-7 Ma) Linxia deposits in
158 China (Li et al. 2014).

159

160 The breeding distribution of the lesser kestrel spans from Iberia and Morocco in the
161 Western Palearctic, to Mongolia and China to the east, always within the temperate belt of

162 Eurasia and northern Africa around the Mediterranean Sea (Negro 1997). Therefore, lesser
163 kestrel distribution overlaps very precisely with that of the ancient civilizations building the
164 first cities (first in the Fertile Crescent, and later in the Middle East and around the
165 Mediterranean at the apex of the Roman Empire in 117 AD) (Kumar 2019). Being a migratory
166 species, the current wintering areas of the lesser kestrel are in sub-Saharan Africa, from
167 Senegal to Chad for European populations (Rodríguez et al. 2009, Sará et al. 2019), and in
168 Kenya and Tanzania, down to South Africa for Asian populations (Wink et al. 2004, Rodríguez
169 et al. 2011). Lesser kestrels do not build a nest but lay their eggs on a ledge or hole. They breed
170 both on natural substrates, including rocky outcrops and cave crevices, and on buildings in
171 rural settings or within urban areas (Negro 1997). The urban habit is typical of the Western
172 Palearctic portion of the breeding distribution, where more than 95% of nest sites are in
173 buildings, either in towns or scattered in isolated constructions in the countryside. Eastern
174 populations in the Asian steppes, however, often nest on rocky outcrops, or even the ground
175 among stone accumulations (Parr et al. 2000). The human populations of the steppes were,
176 and some still are, highly nomadic, and permanent settlements are few, well apart and with no
177 or few large historic buildings.

178 **Data sources**

179 To assess the pre-urban distribution range of the species across time we have used the
180 available fossil record for the species. A catalogue of circa 1.400 sites with Pleistocene
181 avifaunas for the Palearctic was compiled by Tyrberg (1998), with an online supplement
182 (Tyrberg 2008). Additional data were reviewed by Sánchez-Marco (2004). To assess the
183 potential early urban breeding of lesser kestrels in the earliest Iberian cities, we have searched
184 historiographic sources and archeological records. This region has been continuously inhabited
185 since prehistory, with a transition from the Mesolithic to the Neolithic dated about 7.000-
186 6.500 years BP (Alday-Ruiz 2009). The first written sources on kestrels date from Roman times,
187 and have been preserved in much later editions (e.g., Columella (1471) and Pliny the Elderly
188 (Plinius 1469). We have searched these sources for descriptions of kestrel species nesting on
189 buildings.

190 For the different cultural periods after the Romans and before the 19th century, we
191 have researched both building typologies compatible with the presence of lesser kestrel
192 colonies (i.e., constructions with a potential abundance of cavities) and descriptions of bird
193 species and its habits in natural history and falconry works. The lesser kestrel was given species
194 status separate from the Eurasian kestrel (*Falco tinnunculus*) by Fleischer in 1818 (published in

195 Sylvan [Laurop & Fischer] [1817-1818] p. 174). We have compiled references to Fleischer's
196 newly recognized species (i.e., *Falco naumanni*) in Iberia by resident naturalists and foreign
197 travelers all along the 19th century.

198 The first population estimate ever for the species in Spain was given at the ICBP
199 Conference held in 1975 (Garzón 1977), and almost concurrently 14 selected colonies were
200 surveyed by Franco and Andrada (1976) in southwestern Spain. However, the very first
201 nationwide survey was not conducted until 1989 (González and Merino, 1990). Since then,
202 other population estimates have been made in different regions and provinces. One of us (JJN)
203 has monitored lesser kestrels in Andalusia, southern Spain, since 1989 to 2019. Considering
204 that Franco and Andrada's colonies were mainly in Andalusia and were also part of our survey,
205 we have data for a period of 46 years in selected colonies, this making the only long-term
206 study on colony occupancy available for the species so far. The Autonomous Government of
207 Andalusia monitors the population totally or partially (i.e., a subsample of colonies) every two
208 years since 2003. We have had access to all their data and have used them for some of our
209 analyses. For Extremadura, bordering Andalusia to the northwest and also having a large lesser
210 kestrel population (González and Merino 1990), we also have had access to the monitoring
211 data collected under the coordination of the Autonomous Government.

212 **Data Analyses**

213 Using the available databases for lesser kestrel colonies in both Andalusia and
214 Extremadura, we have used construction dates for historic structures (n=349) located on
215 defensive walls, towers, castles, palaces and religious buildings (mainly churches but also
216 chapels, convents and monasteries), and have determined the oldest possible continuous
217 occupation by the kestrels in those structures. We obtained construction dates from different
218 sources including provincial catalogues of historic monuments and municipal archives. In some
219 cases, exact dates are unknown and only an approximate date is given (e.g., 12th century). In
220 case construction works took decades to complete, as with some cathedrals, we used the later
221 date provided.

222 To estimate colony turnover at urban colonies (i.e., colony-desertion rates), we used
223 data for the colonies within our own 46- and 30-years long monitoring schemes.
224 Recolonization of some colonies previously deserted has also been observed and the dates are
225 given.

226 **Distance to cliffs**

227 The vast majority of the lesser kestrel colonies (97.5%, n=1285) in the databases we used are
228 located, or were located if they were deserted during the monitoring period, in human-made
229 structures in cities, towns or in buildings scattered in the countryside. In addition, colony
230 locations were overwhelmingly surrounded by open agricultural land with a predominance of
231 cereal crops and sunflower, which was introduced in Spain as a major culture for oil production
232 in the second half of the 20th century (Negro 1991). Natural substrates where kestrels may
233 establish colonies are rocky outcrops. In Andalusia these are available on the mountain areas
234 on both sides of the Guadalquivir valley, the major river in Andalusia. Andalusia achieved its
235 basic geological layout of today at the onset of the Quaternary, and major cliffs and rocky
236 outcrops in mountain areas were already exposed a long time ago in the Pliocene or early
237 Pleistocene (Rodríguez-Vidal and Gracia Prieto 2004).

238 A majority of the Andalusian colonies are located within the Guadalquivir valley at
239 varying distances from natural cliffs. We have estimated the minimum distance from all
240 colonies to natural cliffs on the borders of the valley to compare it to distances travelled by
241 lesser kestrels during the breeding season (data are available from previous studies), and
242 therefore to infer whether lesser kestrels would have been able to exploit the large
243 herbaceous cultures of the Guadalquivir river should have they kept the original habit of
244 nesting on rocky outcrops.

245 To assess spatial distribution of nesting colonies in relation to cliff availability, we used
246 the complete database of breeding colonies of the Autonomous Region of Andalusia (n = 1,285
247 nesting colonies) and a 100m-resolution slope raster layer available at the Environmental
248 Information Network of Andalusia (REDIAM;
249 <http://www.juntadeandalucia.es/medioambiente/site/rediam>). For each colony, we calculated
250 the distances to the nearest cliff, i.e. pixels with a slope angle equal or higher than 50. Analyses
251 were conducted in *Qgis* version 3.8.2 (Open Source Geospatial Foundation Project,
252 <http://qgis.osgeo.org>).

253

254 **Results**

255

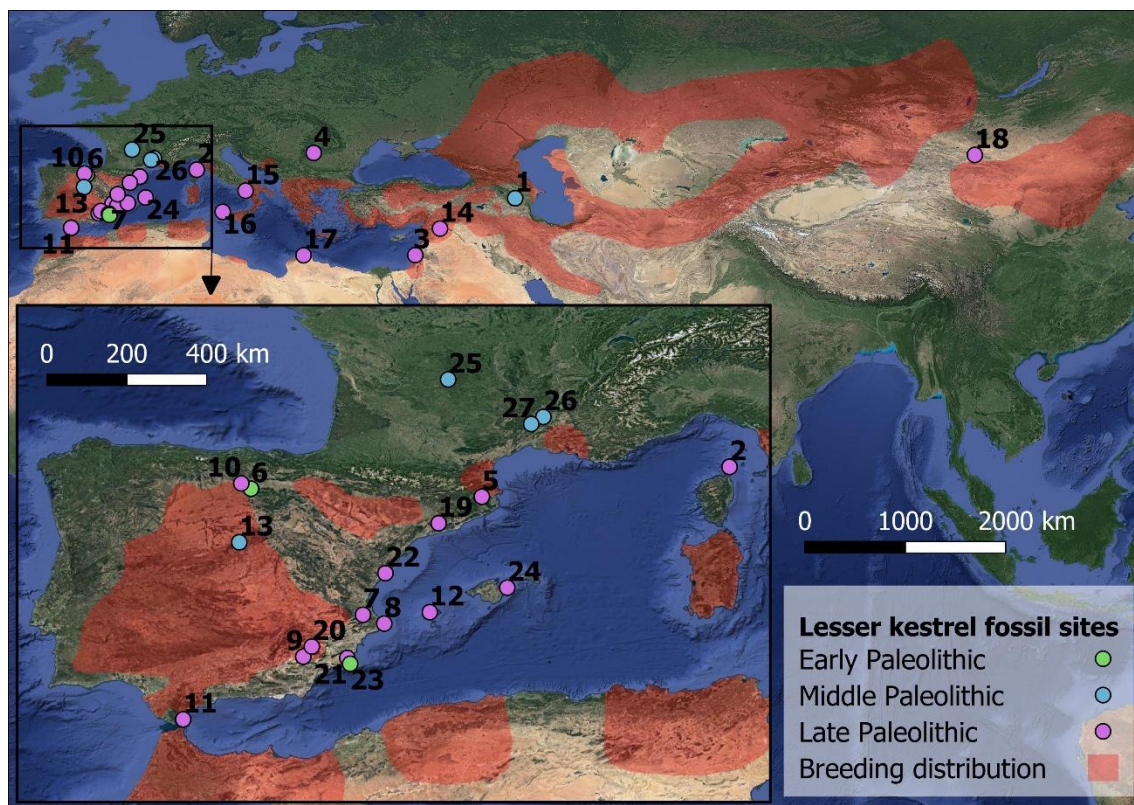
256 **Fossil record**

257

258 The lesser kestrel is a relatively well represented species in paleontological sites (n= 32
259 different sites, including 31 caves and one open site, 47 specimens), with numerous records all

260 across the Mediterranean and to the East, up to the Altai Mountains in Mongolia (Fig. 1). Iberia
 261 and adjacent Balearic islands is the region with a majority of both individual sites (20 sites out
 262 of 32 in our sample) and specimens (65.9%, n=47 specimens, distributed from the early
 263 Paleolithic (about 1 million years BP) to the Epipaleolithic (10,000 years BP), suggesting the
 264 Lesser kestrel may have been present in at least parts of the region all along the Pleistocene,
 265 perhaps taking advantage of the refuge characteristics of Iberia during glacial times. The two
 266 oldest fossils, from the early Paleolithic, were both excavated in Iberia.

267



268

269

270 Fig. 1. Location of fossil remains of lesser kestrel with indication of the date of the layer where
 271 they were found. The current breeding distribution of the species is shown as an ochre shade.
 272 Each number denotes a site. 1. Azykh, Nagorno Karabakh. 2. Grotte de la Coscia, Corsica. 3.
 273 Hayonim Cave, Galilee. 4. Pestera Cioarei, Gorj. 5. Arbreda, Girona. 6. Atapuerca, Burgos. 7.
 274 Cova Negra, Xàtiva. 8. Cova de les Cendres, Alicante. 9. Cueva de Ambrosio, Almería. 10. Cueva
 275 de Valdegoba, Burgos. 11. Gibraltar (5 different caves). 12. Cova des Pouas, Ibiza. 13. Pinilla del
 276 Valle, Madrid. 14. Tell Mureybat, Raqqa. 15. Castelcivita, Salerno. 16. Grotta delle Pecore.
 277 Trepani. 17. Haula Fteah, Cyrenaica. 18. Tsagan Agui, Gobian Altai. 19. Cova de la Guineu,
 278 Guardiola de Fonrubí. 20. Cueva Negra, Murcia. 21. Sima de la Palomas, Murcia. 22. Cau D'en

279 Borrás, Castellón. 23. Cueva Victoria, Murcia. 24. Cova Nova, Capdepera. 25. La Fage, Corrèze.
280 26. Orgnac, d'Orgnac-l'Aven. 27. Salpêtre de Pompignan, Gard.

281

282

283 **Major architectural landmarks through history in Iberia**

284

285 **Pre-Roman period**

286

287 The first cities in Iberia with stone buildings and surrounded by defensive stone walls, a
288 potential substrate for cavity-nesting birds, were built about 5000 years BP (e.g., Los Millares,
289 Aranda-Jiménez 2020). In a later period, just prior to the Roman conquest, cities like Pintia of
290 the Vaccean culture in northern Iberia were protected by 4 m high stone walls which were
291 more than 1 km long and were reinforced with numerous turrets (Sanz et al. 2010). Many
292 other walled cities called *oppida* (i.e., hill fortresses) dotted the landscape (Sanz et al. 2011).
293 However, ancient Iberian cities were destroyed, built over or buried after Roman occupation
294 (starting 2200 years BP), and only some foundations or scattered pieces of walls remain today.
295 No lesser kestrel colonies are currently located in any of the ruins of Iberian settlements, and
296 no kestrel remains have been reported from excavation sites. Although conditions may have
297 been suitable in the past, we lack evidence that kestrels ever bred on ancient Iberian
298 settlements.

299

300 **Roman Hispania**

301

302 Romans built cities and villas extensively in Iberia across 7 centuries (from 200 yr BP to the 5th
303 century). Pliny the Elder recorded 175 towns and villages in the Roman province of Baetica
304 (current Andalusia and southern Extremadura) in the 1st century CE (Plinius 1469), while
305 Claudius Ptolemy mentioned 80 cities in the 2nd century CE (Ptolomeo 1486), a majority of
306 which are still inhabited. The human population for the whole of Hispania may have ranged
307 from 4-6 million people in this period (McEvedy and Jones 1978). Apart from large public
308 buildings such as theaters and temples within major cities, the romans erected colossal
309 infrastructures including aqueducts and stone bridges. Many cities were also surrounded by
310 defensive stone walls, such as the ones encircling the city of Lugo, in northern Spain, that built
311 in the 2nd century are still standing and well preserved. They are 2130 m long, reinforced by 85
312 turrets (Richmond 1931). All these large constructions made of stone, bricks and/or concrete

313 may have provided adequate nesting sites for hole nesting birds, including the lesser kestrel,
314 since the time they were erected. The skeletal remains of a lesser kestrel were unearthed from
315 a roman villa at Tinto Juan de la Cruz (Madrid Province, central Spain), dated in the 1st-5th
316 centuries (García Petit 2017). Romans used terracotta tiles for covering the roofs of their
317 buildings in Hispania, including town houses and villas (García Giménez et al. 2004). Those
318 smaller buildings with tiled roofs would have provided appropriate nesting sites for lesser
319 kestrels, particularly when they were at some point abandoned and the roofs deteriorated.
320 Romans also excavated quarries for construction stone at an industrial scale (Gutiérrez García
321 2012) that may have served as artificial rocky outcrops suitable for cliff-nesting species such as
322 the lesser kestrel (see Fig 10S, supplementary material). Some Roman monuments are still
323 standing or have been partly rebuilt, even if smaller houses all disappeared centuries ago.
324 However, no kestrel colonies are located on Iberian Roman ruins nowadays.

325

326 **Germanic invasions**

327

328 Following Roman domination, Iberia was ruled by the Visigoths and other Germanic
329 peoples who come from central Europe, from the 5th to the 8th century (Collins 2004). Major
330 architectural remnants from this period are stone churches and chapels (pre-romanesque
331 architecture) that may have hold cavity nesting birds on their outer walls and towers.
332 However, as with the preceding periods, no lesser kestrel colonies are currently located in
333 these ancient buildings, all of which have suffered deep alterations through the centuries.
334 Surviving ones have been in fact re-erected practically from scratch with modern restoration
335 techniques in the 20th and 21st centuries.

336

337 **Islamic ruling of Al-Andalus**

338

339 The next major architectural period was brought over by the Islamic peoples who
340 entered Iberia from North Africa starting in the early 8th century (Kennedy 1996). They swiftly
341 established themselves in practically the whole of the peninsula. The muslims built their
342 castles, palaces and mosques on the foundations of the towns and villages previously erected
343 by romans and goths, very often recycling building materials. Muslims defended their
344 settlements erecting either stone walls or using a particular construction technique locally
345 called *tapial* (i.e., rammed earth), which left many regularly spaced holes called *agujales* (Figs
346 1S-2S, supplementary material). Having been erected closer in time to present day, many

347 Islamic city walls and castles are still standing, particularly in Andalusia (southern Spain), where
348 the muslims ruled the Kingdom of Granada until the end of the 15th century (Kennedy 1996).
349 Extant lesser kestrel colonies abound in monuments of the peninsular Islamic period, mainly
350 including castles and defensive walls, the oldest ones built in the 8th century (see fig. 5). We
351 may thus infer potential continuous occupation of buildings by lesser kestrels in the portion of
352 territory ruled by the muslims in Iberia, going back in time up to 1200 years.

353

354 **From the Renaissance to today**

355

356 Christians regained full control of Iberia in 1492 when they conquered Granada.
357 However, they had started to control large areas from north to south in the preceding 2-3
358 centuries (O'Callaghan 2013). The Christians built numerous castles in their advance, as well as
359 churches, monasteries and cathedrals, often enlarging or modifying the mosques and minarets
360 previously erected by their predecessors, as with the cathedral of Sevilla, still holding a lesser
361 kestrel colony known from at least the mid 19th century (see below). This large building
362 complex may have been continuously occupied by lesser kestrels for several centuries, since a
363 mosque was first erected in the 12th century (<https://whc.unesco.org/en/list/383>).

364

365 In Fig. 5 we provide the number of lesser colonies in historical buildings in Andalusia
366 and Extremadura on a century-by-century basis. Since the Middle Age (including Romanesque
367 and Gothic architecture), large public buildings used to be provided with numerous square
368 holes on the walls for securing wooden scaffolding during construction, painting or repair
369 works. These regularly spaced cavities are called putlog holes or putlock holes (mechinales in
370 Spanish) (see Figs. 3S-6S, supplementary material), and lesser kestrels find in them optimal
371 nesting places (Negro and Hiraldo 1993). A majority of kestrel colonies are located today in
372 monuments built in the 16th-18th centuries (Fig. 5), this reflecting the fact that a majority of
373 the largest buildings with suitable nest-sites were erected in the centuries when the Spanish
374 Empire was at its peak in extension and richness (Maltby 2009).

375

376 Lesser kestrels have also established breeding colonies in entirely new buildings
377 erected in the 20th century, both within towns and villages, or in isolated rural constructions
378 such as farmhouses and barns (González and Merino 1990), demonstrating a high adaptability
379 to new types of artificial cavities. Nest-sites are generally under tiled or undulated roofs (Fig.
380 8S, supplementary material), although breeding pairs may use other holes or crevices. In Spain
381 and other Mediterranean countries (e.g., Bux et al. 2008), lesser kestrels have been attracted

382 to modern buildings by placing nest-boxes. Structures similar to dovecotes have been built for
383 kestrels (Fig. 9S, supplementary material), and some have been adopted by the species,
384 particularly if juveniles were released *in situ* following the hacking method (Rodríguez et al.
385 2013).

386

387

388 **Foraging habitat requirements**

389

390 As explained above, nesting habitat in urban environments is a critical aspect for
391 survival in a vulnerable small raptor like the lesser kestrel. But lesser kestrels also heavily
392 depend on open lands for their diet mainly composed of orthopterans (Andrada and Franco
393 1976, Rodríguez and Bustamante 2008). In fact, a trade-off between productivity and survival
394 in rural versus urban colonies, even if both types were on human constructions, was already
395 noted by Tella et al. (1996). Rural colonies in isolated buildings may reach higher productivities
396 of nestlings as foraging trips are much shorter, but may also suffer catastrophic predation of
397 both young and adult birds from *Martes foina* and other predators. Urban colonies may have
398 lower productivity due to longer distances to foraging grounds outside town, but are safer for
399 the birds as they typically lack predators, which are excluded by human presence (Tella et al.
400 1996, Negro 1997).

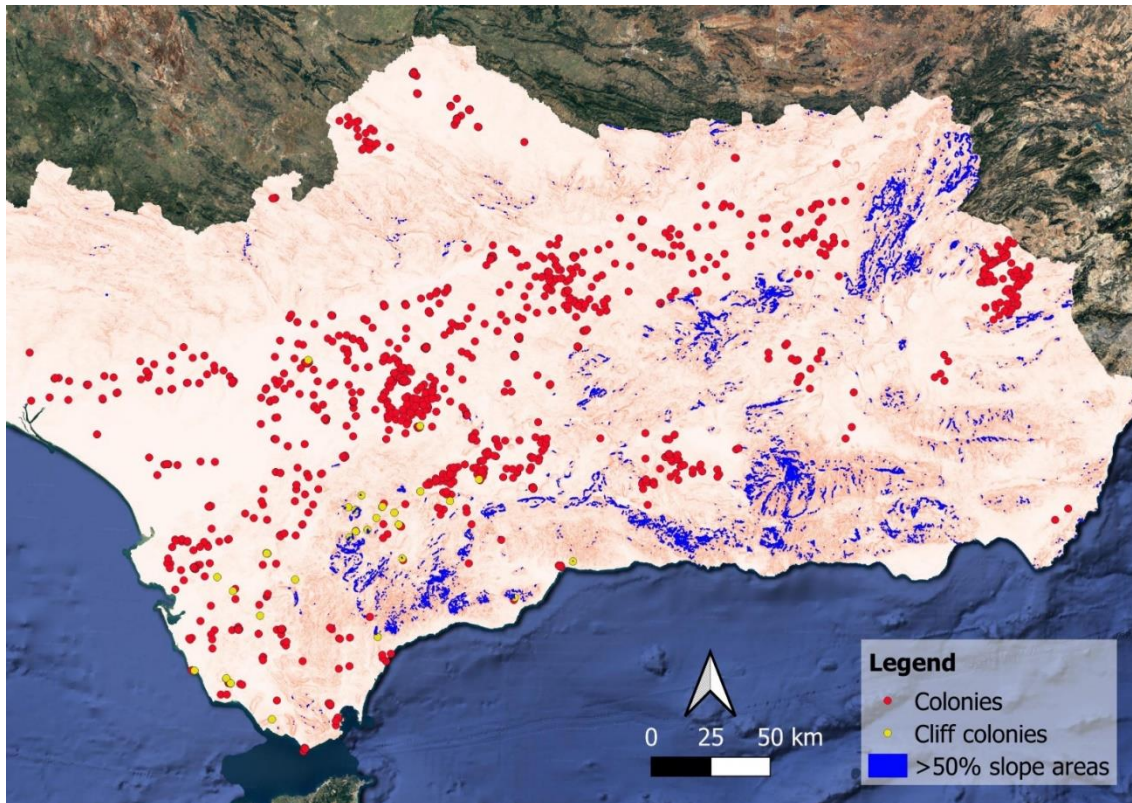
401

402 The building of the first cities in the Neolithic was accompanied by the clearing of land for
403 cereal agriculture (e.g., Summers-Smith 1988). By 3.000 years BP, major agricultural areas
404 today had already been heavily transformed (>20% of the arable land, on average, had been
405 used, Stephens et al. 2019). In Iberia, roman domination implied the ploughing of extensive
406 areas around towns and villas that were possibly as important for the lesser kestrels as the
407 buildings themselves. Major agricultural regions already in Roman times have consistently
408 been cultivated for two millennia until today using essentially two main crops –i.e., cereals and
409 olive trees- in the case of Andalusia, that we use here as an example. Today, a majority of
410 lesser kestrel colonies are located in those heavily cultivated areas in the lowlands of the
411 Guadalquivir river valley (Fig. 2).

412

413 The median of the distance to the nearest natural cliff for all colonies in the region is
414 13 km, with some colonies located more than 40 km away from a natural outcrop (Fig. 3). The
415 mean distance from the nest to the foraging site by kestrels during the chick rearing period is

416 2-3 km (Vidal-Mateo et al. 2019, Cecere et al. 2020). Therefore, the location of a majority of
417 the colonies and their nearest foraging grounds today would be out of reach for lesser kestrels
418 had they kept the habit of breeding in mountainous rocky outcrops.
419



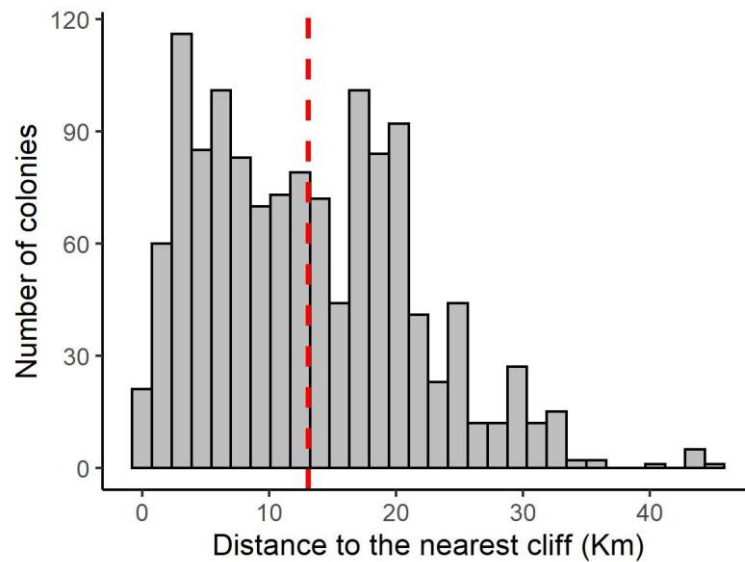
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421

422 Fig. 2. Lesser kestrel colonies on a digital relief model of Andalucía (Southern Spain) in the 21st
423 century (colonies monitored 2003-2019). Red dots: colonies on buildings (n=1252, 97.5%).
424 Yellow dots: colonies on rocky outcrops and coastal cliffs (n=33, 2.5%).

425

426



427

428 Fig 3. Distance to nearest cliff (Km) of lesser kestrel colonies (n= 1285) monitored in 2003-2019
 429 in Andalusia. The red broken line indicates the median distance (13.5 km), exceeded by 50% of
 430 the colonies.

431

432

433 **Urban kestrels in ancient written sources**

434

435 The first written references to kestrel breeding on human buildings are found in
 436 Columella (1471). Columella, who was born in the year 4 CE (Current Era) in Gades (today, the
 437 city of Cádiz in Andalusia), stated that kestrels are small raptors that almost always breed on
 438 the walls of buildings. Quoting Greek author Democritus, Columella also noted that kestrels
 439 may defend rock doves at dovecotes from the attack of larger raptors, and thus help pigeon
 440 breeders to preserve their animals. Lesser kestrels gather to mob both diurnal and nocturnal
 441 birds of prey when at the colonies, but to defend themselves and their progeny. Negro (1997)
 442 described how barn owls *Tyto alba* –known to kill adults in their nests occasionally- provoked
 443 immediate aggregation of adult kestrels (sometimes up to 25) if flying in daytime. Mobbing
 444 kestrels called loudly, diving on the intruder and pursuing it out of the colony (Negro 1997).
 445 Eurasian kestrels *F. tinnunculus* and jackdaws *Corvus monedula* are also driven off when
 446 approaching nest sites (Bijlsma et al 1988). This communal defensive behavior is possibly the
 447 one first described by Democritus and later by Columella. Pliny the Elder, another Roman
 448 naturalist contemporary of Columella who travelled extensively in Hispania, also quotes the
 449 same Democritus' passage on kestrels and pigeons at dovecotes in Book 10th (Chapter 52) in
 450 his *Naturalis Historiae* (Plinius, 1469). Same as suggested for rock doves (see Fig. 4), other
 451 species such as choughs *Pyrhocorax pyrrhocorax* are known to benefit from the collective

452 defense against predators by colonial lesser kestrels when sharing the same buildings (Blanco
453 and Tella 1997).

454

455



456

457 Fig. 4. Lesser kestrels and domestic pigeons standing at the entrance of their nest cavities at
458 Castle of Marchenilla (13th century). Seville province. @Juan J. Negro (2019).

459

460 After the aforementioned classical authors there is a great void, and the next surviving
461 reference to kestrels breeding in “tall buildings, temples, towers and walls” is given by Ulisse
462 Aldrovandi (1599). Almost concurrently, the Portuguese Diogo F. Ferrerira (1616) mentions the
463 existence of two kestrel species, one breeding in towers –possibly the lesser kestrel- and the
464 other one on trees –the Eurasian kestrel-. The Spaniard Gerónimo Huerta (1624) translated
465 Pliny’s Natural History of Animals adding comments and referring to the urban habit of some

466 kestrels. A century later, the Italians Manetti et al. (1767-1776) included the first known color
467 drawing of an adult male lesser kestrel that they called Gheppio di Torre (i.e., Tower Kestrel) in
468 a clear reference to the habit of nesting in buildings. The references given in this and the
469 following section have been incorporated into Fig. 5 to create a timeline for kestrel
470 urbanization according to written sources.

471

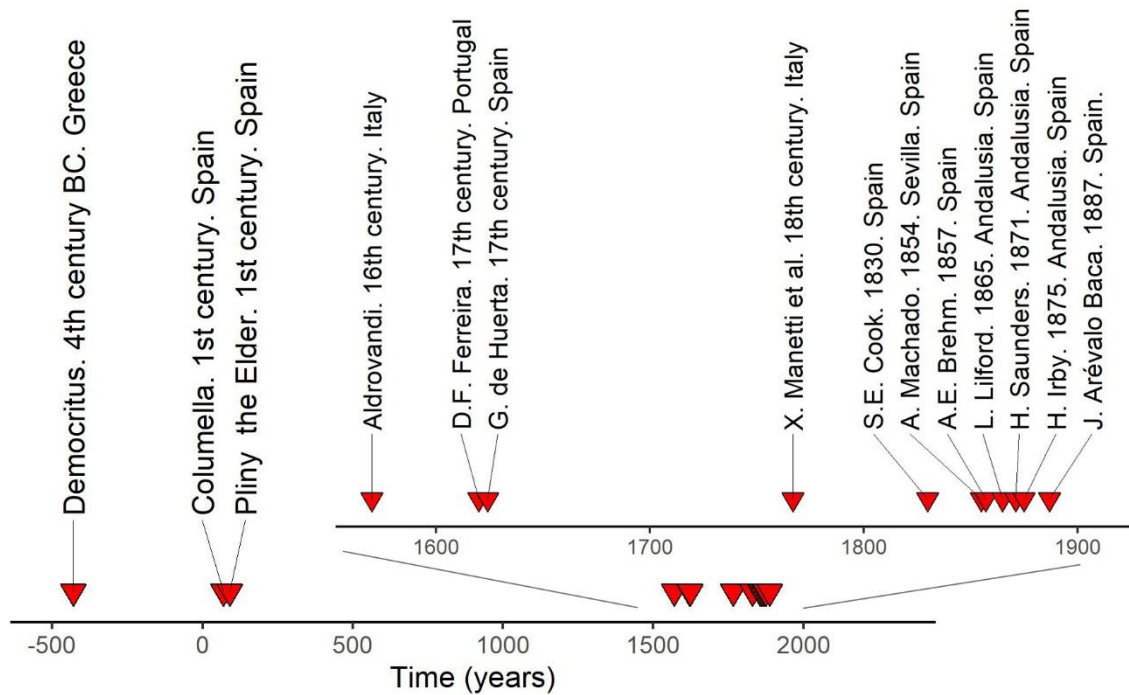
472

473 **References to urban breeding of lesser kestrels in the 19th century**

474

475 The interest for nature and zoology sharply increases in the 19th century with regard to
476 preceding centuries (see Fig. 5). Several foreign and local naturalists attest to the presence of
477 Lesser kestrels breeding in buildings in Spain, mainly in Andalusia, with quotations clearer than
478 any time before, as specific places and dates are given in travelers' books or natural history
479 works. Cook (1834), referring to Andalusia, stated that lesser kestrels "live in the cities,
480 breeding in the lofty towers which have replaced the minarets of the Moors". Machado (1854),
481 noted that lesser kestrels nested in abandoned towers and buildings all across the province of
482 Sevilla, where they were "very common". He undoubtedly referred to the lesser kestrels, and
483 not to the Eurasian kestrel that is sedentary, as Machado correctly specified that urban
484 kestrels arrived from migration in February and left in October. Alfred Brehm (1858), a German
485 zoologist who toured Spain for a year, reported that lesser kestrels were "frequently observed
486 as couples, families and groups in the cities of southern and central Spain, where, as in Athens
487 (Greece), breed in buildings and church towers". He specifically refers to lesser kestrels
488 breeding in belfries in Madrid, Sevilla and Granada. Lilford (1865) stated: "I think, in April and
489 May, the lesser kestrel are the commonest birds in Andalusia, with perhaps the exception of
490 the Bee-eater (*Merops apiaster*). Every church-steeple, belfry, and tower, every town and
491 village, every ruin swarms with them". Saunders (1871) similarly reported that "the birds
492 swarm about old buildings". Irby (1875) a British officer stationed in Gibraltar, noted that vast
493 numbers of lesser kestrels nested on the Rock itself, chiefly on the north face. Also very
494 abundant in rocks and ruins, particularly on the "old Moorish buildings and towers, of which
495 there are so many in Andalusia". In some places, like the city of Sevilla, Irby wrote they "swarm
496 like bees in a hive". The Spanish zoologist Arévalo Baca (1887) recorded lesser kestrels nesting
497 at the Cathedrals of Sevilla and Jerez, where they still do as of 2020. He also mentioned
498 colonies in the Cathedrals of Malaga and Granada, as well as in the Alhambra of Granada and
499 the Alcazar of Segovia in central Spain.

500



501
502

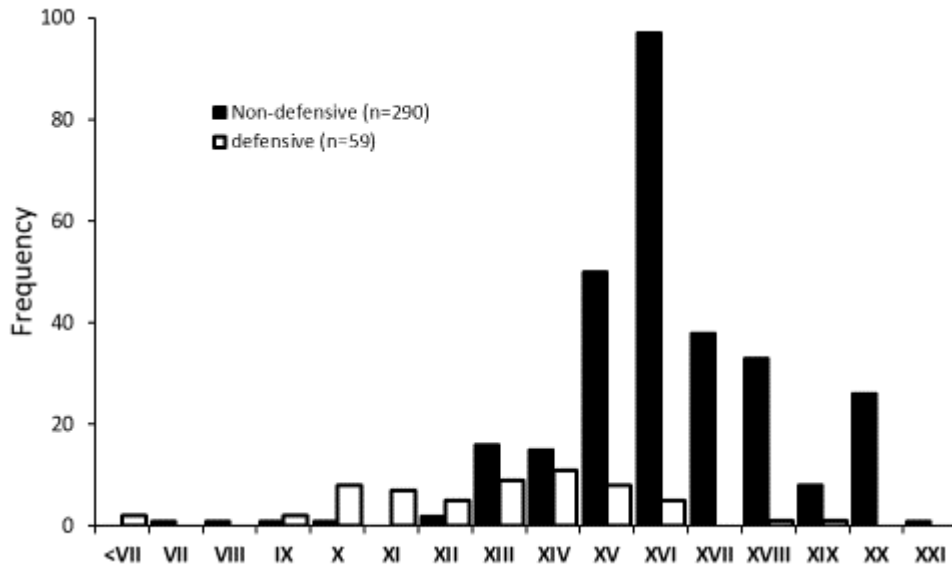
503 Fig. 5. Timeline showing written references to kestrels nesting in buildings. Prior to the 19th
504 century, lesser and Eurasian kestrels were not considered different species, although some
505 authors knew there were urban kestrels and wood kestrels.

506
507

508 **Longest potential continuous occupation of specific colony sites**

509
510

511 A majority of the structures holding kestrel colonies we were able to date (n=349)
512 were erected on the 15th and 16th centuries (Fig. 6). If we assume lesser kestrel established
513 their colonies there right after construction, this give a maximum potential occupation time of
514 500-600 years for those modal structures (mainly religious buildings). The oldest structures of
515 colonies tend to be defensive (i.e., Islamic walls, defensive towers in the countryside and
516 castles). This may also be explained because few of these structures were newly built after the
517 Christian Kings took full control of Iberia after conquering the Islamic Kingdom of Granada in
518 1492. It is also significant that 63% of structures with colonies were built during or before the
519 16th century, and 90% before or during the 18th century. This would agree with the
520 observations in the 19th century (see above), when reports always mentioned presence of
521 kestrels in old buildings, towers and belfries.



522

523

524 Fig. 6. Construction dates (by century until present) of human-made structures in towns or in
 525 the countryside holding lesser kestrel colonies at present (2003-2019). Black columns for non-
 526 defensive buildings (e.g., churches), white columns for defensive walls, towers and castles.

527

528

529 Colony turnover

530

531 We have been able to estimate colony turnover at specific buildings using two
 532 datasets. Franco and Andrada (1976) located 15 lesser kestrel colonies in Andalusia and
 533 Extremadura for a dietary study conducted in 1973. Fourteen of these colonies have been
 534 monitored intermittently until 2019 by JJN. Of these 14 colonies, 4 were deserted by kestrels
 535 for unknown reasons before 1989, although three of them were recolonized after 1995 (21%).
 536 Four disappearing colonies represent a 28% desertion rate in 46 years. The second dataset
 537 comprises 25 colonies in as many different buildings in the province of Sevilla which started to
 538 be monitored in 1989 and up to 2019. Ten (40%) of these colonies have been deserted in the
 539 30 years monitoring period. As for the reasons for colony desertion, in some cases cavity loses
 540 due to restoration work was documented, but in other cases the reasons are unknown.

541

542

543 Discussion

544

545 The Lesser kestrels started to diverge from the remaining of the kestrel lineage
546 between 2-4 million years ago (Fuchs et al. 2015), and we can consider this to be the time the
547 lesser kestrel stands as a separate biological species. The lesser kestrel is a hole nesting
548 species: as with the remaining members of the *Falco* genus (Ferguson-Lees and Christie, 2001),
549 they do not build a nest of their own and directly lay the clutch on a crevice or hole (Negro
550 1997). Natural nest sites excluding buildings or other human-made structures are holes in
551 caves, rocky outcrops, river banks and stone accumulations on the ground (Brehm 1895, Negro
552 1997, Parr et al. 2000). They only rarely nest on tree holes, or on tree nests built by other
553 birds, as done by two other Eurasian small falcons, *F. vespertinus*, and the Amur Falcon, *F.*
554 *amurensis*, that typically nest on unused corvid nests on trees (Ferguson-Lees and Christie,
555 2001).

556

557 Given that the first permanent settlements were built by humans at the onset of the
558 Neolithic, about 10,000 years ago, lesser kestrels have been necessarily nesting on natural
559 substrates other than buildings for more than 99.5% of their evolutionary time as a separate
560 species. The oldest fossil of a lesser kestrel in Iberia, the one at Cave Victoria in Murcia
561 (Tyrberg 2008), is about one million years old, this demonstrating, along with other more
562 recent fossils in other peninsular sites, that lesser kestrels have been regular inhabitants of
563 Iberia in the Pleistocene, and did not necessarily expand their distribution range with the
564 advent of urbanization and agriculture in the Mediterranean.

565

566 In Iberia, the first permanent human cities that may have hold lesser kestrel colonies
567 because they incorporated high stone walls and actual buildings -not huts- were erected about
568 5000 years ago. Again, lesser kestrels became urban breeders in Iberia very late in their
569 lifetime as a breeding species in the region. Nowadays, less than 2.5% of lesser kestrel colonies
570 in Andalusia are located in rocky outcrops, and thus in natural substrates, and a majority is on
571 buildings, whether isolated in the countryside (mainly abandoned farm houses and old castles
572 or ancient defensive towers), or within towns and cities (often on churches and other large
573 such as palaces or convents, as well as remains of defensive walls, but also on inhabited
574 private houses).

575

576 The first written record of kestrels nesting on buildings is that of Columella (1471), who
577 was born and lived in southern Spain. He did not separate the lesser and the Eurasian kestrel,
578 that may have lived in sympatry in the region. From the behavioral description in his work (i.e.,
579 colonial and urban nesting, as well as communal mobbers of larger raptors when nesting on

580 doves) we may infer he was referring to lesser kestrels. Roman built doves similar to
581 the traditional ones made of rammed earth still in use in northern Spain, with a well preserved
582 representation in the Nile mosaic of Palestrina (Central Italy) composed in 100 BC
583 (Germanidou 2015). Lesser kestrels do use them nowadays for nesting (personal observations).
584 Doves are ideal colony structures for kestrels, as the size of the pigeon holes is adequate
585 for them, and coexistence with the pigeons is neutral, as the lesser kestrels never prey on
586 pigeon squabs, and do not disturb the adults. This behavior was essential for the kestrels to
587 have been permitted as wild breeders by dove owners. In addition, doves in Spain
588 have been set in cereal-producing regions, again perfect foraging grounds for these
589 insectivorous kestrels.

590

591 We may set the move of lesser kestrels from natural sites to the cities in Roman times,
592 about two millennia ago in Iberia. Earlier occupation of buildings may have been possible in
593 earlier urban civilizations to the East, in Mesopotamia, Egypt, the Middle East and the Balkans.
594 As we said above, Columella quotes Democritus, a Greek philosopher and naturalist of the 4-
595 5th century BCE when describing kestrels at doves. And the Parthenon in Greece, built
596 precisely when Democritus was born (2460 years BP) has lodged lesser kestrel colonies until at
597 least the 19th century (Brehm 1958).

598

599 Extant lesser kestrel colonies in Andalusia are located in a variety of human-made
600 structures erected in different epochs. However, there are no colonies in the ancient remnants
601 of pre-roman times or Roman monuments, and there are very few in the surviving buildings of
602 the goths until the 8th century. Even if we may assume lesser kestrels were already urban and
603 bred on human constructions, it is not surprising the ruins of those times do no longer hold
604 breeding colonies. A majority of them collapsed over the centuries and have been covered by
605 sediment of refuse. The ruins shown to the public today have all been excavated and partly
606 rebuilt.

607

608 The lesser kestrel colonies on older buildings in Andalusia –and Spain- are the ones on
609 defensive walls and castles of the Islamic period, about 1000 years old. Contrary to
610 constructions from preceding periods, the Islamic ones have been standing for centuries, with
611 or without further repairs. Additionally, Islamic constructions were mainly made of rammed
612 earth and stone ashlar, with numerous *agujales*, which are the ones used by kestrels as
613 nesting sites (Figs. 1S-2S supplementary material). The *agujales* surely permitted the formation
614 of large kestrel colonies, as the ones described by 19th century authors (see results above) in

615 the Andalusian cities and towns. The walls of the city of Seville at the end of the 12th century,
616 in the Almohade period, were 7 km long with 116 turrets, and remained almost intact until the
617 19th century. Such a structure may have potentially lodged hundreds if not thousands of lesser
618 kestrel nest sites, as this colonial species tolerate neighboring couples of conspecifics about 1
619 m apart, this following the average distance between neighboring *agujales* in the walls (Negro
620 and Hiraldo 1993, Negro 1997, Fig. 1S-2S, supplementary material). The size of the lesser
621 kestrel, the smallest Iberian falcon with a body mass of 110-150 g as an adult, makes possible
622 to enter the smallest *agujales*, with a section of about 12x12 cm and 50-80 cm long (Negro and
623 Hiraldo 1993).

624

625 After the Islamic domination period, their basic urban network remained quite
626 unaltered in Andalusia, although new public architecture was built, particularly churches,
627 convents and palaces. Many of these buildings incorporated putlog holes. These putlog holes
628 (see Figs 3S-6S, supplementary material) were slightly larger than the *agujales* (14x 15 cms, see
629 Negro and Hiraldo 1993), but also optimal for a hole-nesting and colonial species such as the
630 lesser kestrels, as any given building or tower used to have hundreds of regularly spaced
631 putlog holes.

632

633 Today, a majority of lesser kestrel colonies take advantage of the remaining putlog
634 holes in large historic buildings. In our sample of dated monuments, a majority of buildings
635 with colonies was erected in the 15th and 16th centuries, this setting a maximum period of
636 occupation for the colonies of 500-600 years. There were possibly kestrels breeding before in
637 other locations in the same towns, but its date of construction indeed determines maximum
638 continuous occupation in every single building. This also brings out the question of possible
639 colony persistence at any given site.

640

641 The concept that some colonies of common birds have been in particular places since
642 time immemorial (see, e.g., use of the term by Nicholson 1929 for heronries in the UK) needs
643 to be narrowed down, as human buildings suffer alterations over the years/centuries due to
644 fires, earthquakes (such as Lisbon's tsunami in 1755, which severely affected many towns in
645 western Andalusia), or they are just rebuilt by the owners. All these events may have made
646 formerly used places unsuitable for kestrels for a number of years, or even permanently. For
647 this reason, we have estimated colony turnover on specific buildings in recent times. Four out
648 of 14 lesser kestrel colonies monitored from 1973 to 2019 in buildings in Extremadura and
649 Andalusia disappeared at some point (28%). In another sample of 25 colonies monitored in

650 towns of Andalusia from 1989-2019, 10 (40%) disappeared. These rates may have been
651 different in the past, and it is also true that lesser kestrels have colonized even modern
652 buildings. Kestrels may also re-colonize formerly occupied colonies that they had deserted at
653 some point. We know of at least 3 colonies in old structures near the city of Sevilla that were
654 used as colonies in the 1970's, become deserted in the 1980's and were re-occupied in the
655 1990's. A fast range expansion and population increase of lesser kestrels was recorded in
656 northern Spain, where the birds occupied isolated constructions that became unused in rural
657 areas at the end of the 20th century (Jovani et al. 2008). All the above suggests, that even if the
658 lesser kestrel population has generally kept its general breeding range, specific colony sites
659 may have changed widely in history, and may not be as stable as certain falcon eyries on
660 natural rock cliffs that have been used for millennia, as some gyrfalcon *F. rusticolus* nest sites
661 in Greenland, which were studied using stable isotopes on guano accumulations and are
662 considered "ecological magnets" (Burnham et al. 2009).

663

664 According to witnesses' accounts (see references above), individual lesser kestrel
665 colonies possibly numbered hundreds of couples, and maybe thousands, in large fully walled
666 cities such as Sevilla up to the 19th century, or even the first half of the 20th century in certain
667 Andalusian towns (see, e.g., the observation of hundreds of kestrels at Arcos de la Frontera in
668 Cadiz province by Riddell 1945). Nowadays, the largest colony in Spain is the one at the castle
669 of Mairena del Alcor (Sevilla province) with 92 couples in 2020 (Bustamante et al. 2020). The
670 colony on the Islamic walls and castle of Niebla (Huelva province) reached 300 couples at the
671 onset of the 21st century, although it has decreased sharply in recent years (JJN personal
672 observations). But the largest urban colony today is in the Italian medieval town of Matera,
673 with about 1000 breeding couples (Cecere et al. 2020). These numbers give an idea of how
674 large urban lesser kestrel colonies may have been up to a recent past.

675

676 Nesting habitat suitability is by no means the only factor determining the distribution
677 of kestrels in the landscape. Churches and castles with an abundance of holes were also
678 erected in towns located in mountain areas of Andalusia and Extremadura, but they hold no
679 kestrel colonies (personal observations). Our analysis of colony location with regard to natural
680 rocky outcrops outlines the importance of adequate foraging grounds for the species, which in
681 Spain and other Mediterranean countries in the Western portion of its distribution is very
682 dependent on herbaceous cultures (Negro 1991, Negro 1997, Rodríguez and Bustamante
683 2008). Lesser kestrels became largely urban, and still are in 'agro-cities', where they found
684 both suitable nest sites safe from a majority of their predators (Tella et al. 1996), but also

685 because they were close to adequate open habitat during the breeding season. Agro-cities
 686 were largely developed during the Roman domination period in southern Iberia (encompassing
 687 both Andalusia and Extremadura), and the Roman city map has remained almost intact over
 688 successive periods until today. The fact that numerous colonies are also established on
 689 scattered buildings in the countryside indicates that within-town breeding is not the only
 690 human-dependent strategy of lesser kestrels, and that the availability of prey nearby is also an
 691 essential component in the choice of nesting substrates. In rural areas of Hispania, major land-
 692 ownership rested on the Roman “villa rustica” (= farmhouse), which led to the Islamic
 693 “alquería”, and the modern “cortijo” or “hacienda” (Vidal Teruel et al. 2010). Recently
 694 abandoned cortijos (in the late 20th and early 21st centuries) hold numerous small lesser kestrel
 695 colonies in the countryside of both Andalusia and Extremadura today (Bustamante et al. 2020).
 696

697 Kestrels have thrived in cities for centuries, but today their urban habit is threatened
 698 because cavities are increasingly limited, and due to their dependence on suitable agricultural
 699 areas in the periphery of the city for food. In Spain, they deserted major cities such as Madrid
 700 decades ago (Bernis 1974), possibly because foraging trips become too long and unprofitable
 701 among the colonies located in the downtown area and the agricultural fields in the outskirts of
 702 town. An additional and novel cause of concern is posed by invasive species, such as the ring-
 703 necked parakeet (*Psittacula krameri*), that outcompetes the kestrel and claims traditional
 704 kestrel nests for itself (Hernández-Brito et al. 2014). To ensure the millennial urban presence
 705 of lesser kestrel in their Western Palearctic breeding range we have to protect both the
 706 integrity of the buildings holding colonies and the fields where they forage, that ought to be
 707 clean from pesticides for an adequate food supply (Negro et al. 1993).
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997 JJN. conceived and designed the study with input from all other authors. JJN, JP, JJF and AR
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1001

1002 **ADDITIONAL INFORMATION**

1003 **Competing Interests:** The authors declare no competing interests.