

1 Long-term persistence of conservation-reliant species: challenges 2 and opportunities

4 Highlights

- 5 • Artificial nests are increasing Lesser Kestrel and European Roller
6 populations in Portugal
- 7 • All semi-natural nests are expected to disappear by the end of this century
- 8 • Lesser Kestrels and Rollers will become fully reliant on artificially
9 provided nests
- 10 • Nest provisioning to sustain current populations would require 4500€
11 every year
- 12 • These costs are less than 1% of the region's tourism annual lodging income

14 Abstract

15 “Conservation-reliant species” – those fully dependent on continued management actions – are
16 booming and, with limited conservation budgets, securing funds to sustain their long-term
17 viability is becoming overwhelming. This study assesses the degree of dependence on
18 conservation actions of two obligatory cavity-nesters, the Lesser Kestrel *Falco naumanni* and
19 the European Roller *Coracias garrulus*, whose populations in Europe were recently recovered
20 through artificial nest-site provisioning. Using long-term monitoring data and population
21 surveys conducted in their main Portuguese stronghold, we examined temporal changes in the
22 availability and use of semi-natural (cavities in rural abandoned buildings) and artificial nest-
23 sites. We further assessed the financial costs of nest-site provisioning and evaluated the
24 potential use of tourism revenues as a conservation funding source. Following the
25 implementation of conservation projects, the Lesser Kestrel and Roller populations have been
26 increasing but more than 65% of all breeding pairs currently nest in artificial nest-sites. Semi-
27 natural nest-sites remain suitable for approximately 30 years and are expected to disappear by
28 the end of this century. Lesser Kestrels and Rollers will thus become fully dependent on
29 artificial nest-sites and sustaining their current population sizes is estimated to cost 4500€ per
30 year. This represents less than 1% of the region's lodging income, largely supported by nature-
31 based tourism. Our findings suggest that reactive conservation measures can be very effective
32 at recovering endangered populations but can make them fully reliant on the perpetuation of
33 those measures. This demands long-term funding, which can be alleviated by tourism revenues
34 in areas with high nature capital values.

35 **Keywords:** European Roller, Lesser Kestrel, Conservation, Artificial nests, Tourism,
36 Funding

38 1. Introduction

39 Human activities are transforming the face of the planet and causing dramatic changes to the
40 distribution and abundance of wildlife species, mainly through habitat destruction and climate

41 change (Pimm & Raven, 2000; Sala et al., 2000). The decline of biodiversity detrimentally
42 impacts ecosystems and the services they provide which are essential to humans (MA, 2005;
43 Barnosky et al., 2017; Butchart et al., 2010; Cardinale et al., 2012). Increased recognition of
44 the magnitude of human-mediated impacts on nature has prompted large-scale conservation
45 efforts aiming at halting and reversing ongoing biodiversity loss, often incurring high financial
46 costs (e.g. USD 6 billion/year to manage protected areas; Butchart et al., 2006; James et al.,
47 2001). Although conservation actions help prevent extinctions and improve population trends
48 (Butchart et al., 2006; Hoffman et al., 2010; Rodrigues, 2006), funds available are usually
49 insufficient to offset the major drivers of extinction risk (Hoffman et al., 2010; Sebastián-
50 González et al., 2011; Watson et al., 2014).

51 Often priority is given to species and populations that are already highly endangered, focusing
52 on reversing negative impacts in the short term (Cardador et al., 2015; Drechsler et al., 2011).
53 Therefore, conservation approaches are often reactive rather than proactive. Generally, funding
54 is constrained in time, limited to the duration of specific programs and/or achievement of
55 successful results, and is then allocated to new conservation priorities (Scott et al., 2010). In
56 the long-term, reactive conservation may be more expensive than a proactive approach
57 (Drechsler et al., 2011) and can lead to conservation traps by promoting an unsustainable need
58 to perpetuate the implementation of active conservation actions (Cardador et al., 2015). The
59 number of “conservation-reliant species” – those requiring continued, long-term management
60 actions and investment – is likely to increase, stretching even further the limited conservation
61 budgets. Hence, cost-efficient actions that guarantee the economically sustainable conservation
62 of threatened populations are urgently needed (Scott et al., 2010; Sebastián-González et al.,
63 2011).

64 Conservation reliance may be particularly prevalent in human-dominated landscapes, where
65 species have adapted to traditional human activities which have changed dramatically during
66 the last century, the prime example being agriculture intensification (Green et al., 2005; Tilman
67 et al., 2011). As a consequence of these changes, agricultural areas hold many endangered
68 species, and birds associated with farmlands are among those declining the most (Fischer et
69 al., 2010; Socolar et al., 2019; Sodhi et al., 2010; Stanton et al., 2018; Traba & Morales, 2019).
70 Agricultural and other human-dominated landscapes therefore have high levels of biodiversity,
71 often establishing a strong natural and cultural heritage with high aesthetics, ecological and
72 recreational values (Hartel et al., 2014; Schulp et al., 2019).

73 In areas with high biodiversity or recreational values, conservation programmes can be
74 maintained by the financial income generated by tourism (Steven et al., 2013; Walpole &
75 Leader-Williams, 2002). Nature-based tourism, especially when paired with easy-to-see and
76 charismatic species, has great potential to raise funds and awareness for conservation
77 (Czajkowski et al., 2014; Steven et al., 2013; Walpole & Leader-Williams, 2002). Revenues
78 can be raised from accommodation, donations or nature-related activities such as birdwatching.
79 Worldwide, avitourism is a rapidly expanding subsector of the tourism industry and may foster
80 sustainable tourism and nature conservation by reducing the need for external (e.g.
81 governmental) funding (Czajkowski et al., 2014; Kiss, 2004; Steven et al., 2013).

82 The Lesser Kestrel (*Falco naumanni*) and the European Roller (*Coracias garrulus*, hereafter
83 Roller) are two charismatic bird species and icons of nature conservation. Both species suffered
84 major population declines in their European breeding ranges (ca. 46% in each decade since
85 1950s for Lesser Kestrels; 4-20% over three generations for Rollers) and were classified as
86 “Vulnerable” and “Near Threatened, respectively, during the first decade of the twenty-first
87 century (BirdLife International, 2019). The observed declines triggered an increase in
88 conservation efforts that contributed to remarkable recoveries in many European countries,

89 with both species being downlisted to “Least Concern” (although some national populations
90 are still declining; Bux et al., 2008; Catry et al., 2009; Finch et al., 2018; Kovacs et al., 2008;
91 Rodríguez et al., 2011; BirdLife International, 2019).

92 Like many bird populations in human-dominated landscapes, Lesser Kestrels and Rollers are
93 limited by lack of suitable foraging and nesting resources and conservation strategies have
94 focused on promoting environmentally friendly habitat management and nest-site provisioning
95 (Catry et al., 2013; Finch et al., 2018; Franco et al., 2005; Newton, 1998; Rodríguez et al.,
96 2011). Being secondary cavity nesters, they are unable to excavate their own cavities and are
97 thus particularly vulnerable to shortage of nest-sites. Compelling evidence has been found for
98 the effectiveness of nest-site provisioning as a reactive conservation tool to increase population
99 numbers of many endangered species (Lambrechts et al., 2010; Mainwaring, 2011; Newton,
100 1994; Sutherland et al., 2018). Whilst the quick success of artificial nest-site provisioning
101 enabled the fast recovery of Lesser Kestrel and Roller populations throughout Europe, the long-
102 term costs of increased dependency of conservation actions, essential for the persistence of
103 these species, has never been evaluated.

104 In this study we assess the degree of dependence Lesser Kestrels and Rollers have on
105 conservation actions and discuss evidence-based perspectives for their long-term conservation.
106 Using long-term monitoring data, we estimate population trends of Portuguese Lesser Kestrels
107 and Rollers, quantify their dependence on artificial nest-sites and understand temporal changes
108 in the availability of semi-natural ones (cavities in rural abandoned buildings). We then
109 calculate conservation costs associated with artificial nest-site provisioning and compare them
110 with tourism revenues for the region. We aim at illustrating the potential challenges of relying
111 on reactive approaches that may lead to conservation-reliant species, but also the opportunities
112 that arise from tourism to create self-sustainable conservation strategies.

113

114 **2. Methods**

115 **2.1 Study area and species**

116 We focused our study in the Castro Verde Special Protection Area (SPA), located in southern
117 Portugal (37°43'N, 7°57'W). With a total area of ca. 85 000 hectares, it is an important SPA
118 for steppe birds at the European level and one of the main strongholds for several threatened
119 farmland bird species in Western Europe (Moreira et al., 2007). Land use within the SPA has
120 remained relatively stable in the last decades, in part due to the implementation of agri-
121 environmental policy schemes and funding mechanisms that ensure high-quality foraging
122 habitat for many farmland birds (Catry et al., 2013; Silva et al., 2018). This area harbours
123 roughly 80% of the national breeding populations of Lesser Kestrels (418-436 pairs in 2007;
124 Catry et al., 2009) and Rollers (52-55 pairs in 2009; Catry et al., 2011b), where both species
125 have recently reversed declining population trends after the implementation of conservation
126 programs (Catry et al., 2009; Catry et al., 2011b). Together with other key bird species (e.g.
127 Great Bustard (*Otis tarda*), Little Bustard (*Tetrax tetrax*), Black-bellied Sandgrouse (*Pterocles*
128 *orientalis*), Iberian Imperial Eagle (*Aquila adalberti*)), Lesser Kestrels and Rollers are
129 significant contributors to birdwatching and nature-related activities in the region.

130 Lesser Kestrels and Rollers are long-distance Afro-Palaearctic migratory species (BirdLife
131 International, 2019) and opportunistic cavity nesters. The Lesser Kestrel – a cliff-nesting
132 colonial raptor, benefited from the human occupancy of the landscape, both for foraging and
133 breeding, nesting in isolated farmhouses or castles and churches in villages or towns and
134 feeding on invertebrates in farmland areas (Catry et al., 2009). Rollers are solitary breeders,

135 nesting in woodpecker cavities in trees or sandy banks, but can also occupy human buildings
136 in southern latitudes, mainly where trees are lacking (Rodríguez et al., 2011). Most of the
137 population of both species in the study area (around 300-400 and 40-50 breeding pairs of Lesser
138 Kestrels and Rollers, respectively) have been annually monitored since 2000 by the authors
139 and long-term demographic information (number of nests, eggs, chicks) is available.

140 **2.1.1 Semi-natural and artificial nest-sites**

141 In the Castro Verde SPA, there are no records of birds breeding in the original natural nests
142 (burrows in cliffs or hollows in trees). First known settlers nested in abandoned rural buildings
143 (such as houses or farm sheds), traditionally built with adobe (a mixture of lime and mud) and
144 Arabic tiles. After abandonment or lack of maintenance, these buildings decay due to the
145 eroding action of wind and rain, leading to the formation of cavities in walls or under roof tiles,
146 opportunistically used by both species to breed. Because these cavities are not true natural
147 nests, we hereafter refer to them as semi-natural nest-sites. Contrarily to traditional buildings
148 (built at least partially with adobe walls and Arabic tiles, thus potentially providing semi-
149 natural nest-sites), new buildings are made with long lasting materials, such as bricks and
150 concrete, that do not provide suitable cavities for nesting.

151 Since 1998, with the help of funding from European Union (EU) LIFE-nature conservation
152 programmes, artificial nests have been provided to reverse declining population trends of both
153 species (Catry et al. 2009, 2011b). New artificial nests include cavities in plastered walls (new
154 cavities dug in existing traditional buildings that are then plastered), clay-pots and wooden
155 nest-boxes in both traditional and new buildings, and newly built breeding walls and towers
156 with up to 87 cavities each (Catry et al., 2009). In 2017, there were 944 artificial nest-sites
157 available including 149 cavities in plastered walls, 663 in newly built breeding walls and
158 towers, 65 clay-pots and 89 wooden nest-boxes. Lesser Kestrels and Rollers use all types of
159 nests provided, can be often found in the same structures and can use the same nest-sites in
160 alternate years (Catry et al., 2015).

161

162 **2.2 Species surveys, population trends and occupation rate of artificial nest-** 163 **sites**

164 During the 2017 breeding season, the overall area to be prospected within the SPA included
165 open/agricultural areas selected using the Corine Land Cover 2000 map. All human made
166 buildings (including traditional and new buildings: houses, farm sheds, churches, mills, ruins,
167 etc) were selected from military maps at 1:25,000 scale. Buildings not reported in the military
168 maps (e.g. recent ones) but detected during fieldwork were also visited. Besides visiting
169 buildings, all artificial nest-sites provided (including wooden nest-boxes attached to
170 electric/telephone poles or trees) were checked for the presence of both species. Every structure
171 was visited twice to increase the likelihood of species detection: the first visit took place
172 between 24 April and 15 May and the second one between 16 May and 15 June. Whenever the
173 presence of Lesser Kestrels and/or Rollers was confirmed in a structure, the number, location
174 and type of nests (semi-natural or artificial) was recorded. The second visit was made during
175 the chick rearing period to confirm the number of breeding pairs (and control for late breeders
176 or failed nesting attempts, for example), resulting in minimum and maximum estimates of
177 breeding pairs per site. The estimated population size obtained in this survey, along with the
178 proportion of pairs breeding in semi-natural and artificial nests, was then compared with past
179 population censuses (Lesser Kestrel: 2003 to 2007, Catry et al. 2009; Rollers: 2004 and 2009,
180 Catry et al. 2011b).

181

182 **2.3 Temporal changes in nest-site availability**

183 In traditional buildings holding Lesser Kestrel and Roller pairs, nest shortage is an increasing
184 threat due to building collapse (structures are only maintained through frequent conservation
185 interventions to secure walls and roof sections). Whilst longevity of traditional buildings is
186 unknown, Catry et al. (2009) reported that 30% of roofs from buildings monitored for Lesser
187 Kestrels collapsed within a 5-year period and 35% of buildings holding colonies were at high
188 risk of collapse.

189 To understand how the suitability (for cavity nesters) of traditional buildings changes with
190 time, we modelled the relationship between colony size (number of breeding pairs) and time
191 (years) using a dataset from 14 buildings occupied by Lesser Kestrels and monitored for a
192 period of 18 years (authors, unpublished data). Each building was classified according to its
193 degradation level, and in some years, major walls or roofs collapse and colonies disappeared.
194 Once a building is abandoned, we predict colony size will increase initially, as new nest-sites
195 appear with the gradual degradation of the structure, but once a certain decay threshold is
196 reached, the number of cavities declines and the structure begins to lose its nest-sites. We used
197 a smoothing-splines mixed-effects model ('sme' package in R, Berk 2018) to assess changes
198 in colony size along the building degradation process. This model uses smoothing-splines to
199 adjust the relationship between colony size (in proportion to the maximum colony capacity)
200 and time (years), using colony ID as a random factor (Berk, 2018). The optimal model (with
201 the correct level of smoothing) was selected according to the AIC.

202 Moreover, the number of future suitable traditional buildings for Lesser Kestrels and Rollers
203 was estimated using a dataset of 175 randomly selected traditional buildings (corresponding to
204 56% of all traditional buildings in the area) for which suitability (presence or absence of
205 available nest-sites) was assessed in 2008 and 2017. Buildings were considered suitable if they
206 had at least one nest-site available (this was the only significant variable determining if a
207 building can be used by kestrels and Rollers; see Appendix 1 for results of the logistic
208 regression). Non-suitable buildings lack nest-sites and are generally inhabited by humans or in
209 good conditions but may become suitable for nesting following decay. We quantified the
210 number of buildings that became suitable (gained nest-sites following decay) and unsuitable
211 (lost all nest-sites following structure restoration or collapse) from 2008 to 2017 and, assuming
212 the rate of change between these years to be constant, determined the number of suitable
213 buildings until the end of this century (using simple cross-multiplications).

214

215 **2.4 Financial costs of artificial nest-sites and the potential contribution of** 216 **local tourism revenues**

217 To estimate the funding required for the conservation of Lesser Kestrels and Rollers in the area,
218 we calculated the costs associated with the provision of artificial nest-sites needed to sustain
219 the current population size of both species (600 and 60 breeding pairs of Lesser Kestrels and
220 Rollers, respectively), assuming the progressive disappearance of all semi-natural nest-sites
221 (through the collapse of traditional buildings). We estimated the number and cost of nest-sites
222 needed in each decade until the end of the century, maintaining the current proportions of each
223 nest type (costs of each type of nest are presented in the Appendix 2). Calculations were made
224 for all three types of artificial nest-sites found in the area – breeding walls, clay pots and
225 wooden nest-boxes – considering the carrying capacity (number of pairs each structure can

226 hold), estimated longevity, production costs and occupation rate (based on data from 2017).
227 The longevity of wooden nest-boxes and clay pots was estimated based on their average
228 observed longevity in the last 20 years, and concrete breeding walls were assumed to last up to
229 50 years. We only considered costs directly associated with the provisioning of nest-sites
230 (material, labour, transportation). Maintenance of provided nests (cleaning nest-sites before
231 and/or after each breeding season, adding substrate to the nest, or occasionally fixing or
232 replacing lids) were not included in the estimated costs because they are marginal when
233 compared to the overall costs (less than 5% of the yearly provisioning costs).

234 We explored if tourism revenues could contribute to fund the long-term persistence of Lesser
235 Kestrels and Rollers in the Castro Verde SPA. Local, regional and national tourism growth
236 rates were quantified for the period between 2001 – the year before the beginning of
237 conservation projects in the area – and 2017. We used accommodation-related metrics as our
238 measure of tourism. Number of guests, number of nights, and lodging income (total amount
239 paid by guests for accommodation) were retrieved from the Portuguese National Institute of
240 Statistics (INE, 2002, 2008). Albeit not a direct measure, accommodation related metrics are
241 easy to interpret and thus a good indicator of tourism (Rodríguez-Rodríguez & López, 2019).
242 We then compared the Castro Verde Lodging income with the total annual funding required to
243 sustain the current populations of Lesser Kestrels and Rollers.

244 **3. Results**

245 **3.1 Species surveys, population trends and occupation of artificial nest-sites**

246 A total of 412 structures were surveyed in 2017 in the Castro Verde SPA, including 388
247 buildings, 11 breeding walls and 13 isolated wooden nest-boxes placed on electric poles or
248 trees. Of all structures, 151 (37%) were suitable (with at least one suitable cavity) and 67 (16%)
249 structures were occupied by Lesser Kestrels or Rollers (54 by Lesser Kestrels, 43 by Rollers).

250 Lesser Kestrel and Roller population sizes were estimated at 577-625 and 58-60 breeding pairs,
251 respectively. Both species showed increasing population trends in the study area since 2004:
252 Lesser Kestrels increased 177% and Rollers 166% (Fig. 1). Lesser Kestrel colony size ranged
253 from 1 to 80 breeding-pairs and the number of Rollers nesting in the same structure varied from
254 1 to 3 pairs. The proportion of pairs occupying artificial nest-sites also increased substantially:
255 in 2017, 68% of all Lesser Kestrels and 66% of all Rollers were nesting in artificial nests (Fig.
256 1). The most used artificial nest-sites were breeding walls and towers (Lesser Kestrels and
257 Rollers) and wooden nest-boxes (Rollers) (Table A3).

258

259 **3.2 Temporal changes in nest-site availability**

260 Long-term data of Lesser Kestrels breeding in traditional, adobe-made, buildings suggest that
261 these are ephemeral, hosting a Lesser Kestrel colony for an average of 30 years (Fig. 2).
262 Initially, colonies grow as the structure progressively decays and offers more cavities, with the
263 maximum number of pairs ca. 15 years after colonization. After that, the structure decays
264 rapidly and the number of breeding pairs is reduced by 50% just five years after peaking (Fig.
265 2).

266 From the 175 traditional buildings classified as suitable for Lesser Kestrels in 2008 and visited
267 during 2017, 14 became unsuitable due to building collapse, 73 remained suitable, and 88
268 remained unsuitable but may still become suitable in the future due to ongoing or future
269 degradation. The number of suitable buildings is expected to decrease in the future, either due

270 to building collapse or restoration that prevents the establishment of new cavities. Based on the
271 differences recorded between 2008 and 2017, we estimate that the number of new suitable
272 buildings will not be able to offset those collapsing in the next couple of decades, and all
273 traditional buildings, and hence all semi-natural nest-sites, are likely to disappear by the end of
274 this century (Fig. 3).

275 **3.3 Financial costs of artificial nest-sites and the potential contribution of** 276 **local tourism revenues**

277 Sustaining the current breeding populations of Lesser Kestrels and Rollers in artificial nests
278 will cost approximately 4500€/year. This corresponds to 3260 artificial nest-sites that would
279 need to be provided until the end of this century (ca. 360 000€, not accounting for inflation,
280 Fig. 4), including the replacement of existing artificial nest-sites, the provisioning of new ones,
281 and keeping the current ratio of each artificial nest-site type (please refer to figure A1 in the
282 Appendix 2 for additional estimates considering only one type of artificial nest-site). There
283 were differences in the cost per breeding pair between type of artificial nest provided (Kruskal-
284 Wallis $H(2)=8.33$, p -value= 0.016), with breeding walls being more expensive than clay pots
285 (difference in 2.40€, post hoc Tuckey test: $p= 0.023$) (Table 1).

286 Between 2001 and 2017, the number of tourist guests grew twice as fast in Castro Verde than
287 in the South Alentejo region and 3 times higher the average of the full country, with an increase
288 in 572.9% in lodging income (Table 2). In 2017, the income from lodging alone was 794 000€
289 in the Castro Verde area. The funds required to sustain Lesser Kestrels and Rollers in the area
290 thus represent 0.6% of the income generated by this sub-sector of tourism.

291

292 **4. Discussion**

293 **4.1 Artificial nest-sites as a reactive conservation tool**

294 In this study we have shown that a reactive conservation approach – artificial nest-site
295 provisioning – enabled a fast recovery and increase of Lesser Kestrel and Roller populations
296 but made them increasingly conservation-reliant – currently more than 65% of all breeding
297 pairs nest in artificially provided nests. Reactive conservation approaches like this may create
298 long-term conservation traps that have been overlooked by researchers and conservationists
299 but have major implications for the conservation of threatened populations (Cardador et al.,
300 2015; Scott et al., 2010). There is evidence that populations of Lesser Kestrels and Rollers
301 across their breeding ranges could be limited by the number of available nest-sites and
302 providing artificial nests has proven to be an effective conservation tool, responsible for
303 observed recoveries in many European countries (Iñigo & Barov, 2010; Kovacs et al., 2008)
304 and contributing to the down-listing of the species conservation status to Least Concern
305 (BirdLife International, 2019). We must emphasize that the availability of high-quality
306 foraging habitats in the vicinity of the nests is also critical for maintaining positive population
307 trends (Catry et al., 2013; Finch et al., 2018). Indeed, deterioration of foraging habitat has
308 already been pointed out as the major driver of Lesser Kestrel’s population declines outside
309 our study area, even with the provision of artificial nest-sites (Catry et al., 2013). Whilst the
310 extent to which both species are dependent on artificial nests across their range is unknown,
311 other populations around Europe may face similar challenges (Kovacs et al., 2008; Rodríguez
312 et al., 2011; Finch et al., 2018) and to maintain the population numbers of both species, artificial
313 nests will need to be constantly provided and maintained. Our results show that the costs of

314 maintaining healthy populations of Lesser Kestrels and Rollers could be compensated by the
315 economic benefit provided by tourism.

316

317 **4.2 Ephemerality of natural nest-sites and artificial nest-sites as conservation** 318 **traps**

319 Previous studies have already suggested that traditional buildings in the area represent
320 temporary nest resources for birds, either due to their collapse or restoration (Catry et al., 2009;
321 Franco et al., 2005). This study quantifies the longevity of traditional buildings and predicts
322 the decline in number of semi-natural nest-sites over time. Traditional adobe buildings are only
323 able to host Lesser Kestrels' colonies for roughly 30 years before collapsing. Indeed, in the last
324 2-3 years, three out of the 14 Lesser Kestrel colonies included in Figure 2 disappeared, and two
325 were only sustained due the provision of artificial nests (authors' personal observation).

326 At the current rate of movement of people from rural to urban areas, and assuming every
327 structure currently without cavities (mostly inhabited or in good condition) would become
328 suitable in the future, all traditional buildings and, consequently, all semi-natural nest-sites, are
329 expected to disappear before the end of this century. Whilst we should acknowledge some
330 limitations to our projections due to the assumption of constant rate of degradation across time
331 (based on the rate of change observed between 2008 and 2017), the non-reversible loss of
332 suitable traditional buildings, and hence of all semi-natural nest-sites in the short/medium-term
333 seems unequivocal. In fact, suitable adobe-made buildings may cease to exist even sooner, as
334 some may be restored or collapse before the appearance of nest-sites. Adobe is no longer used
335 as a building material in the study region, which precludes the appearance of new adobe-made
336 buildings, potentially suitable to host new colonies in the future. Therefore, the long-term
337 persistence of Lesser Kestrels and Rollers in Castro Verde will soon be fully reliant on artificial
338 nest-sites. The disappearance of semi-natural nests and the logistic effort to ensure the
339 provisioning of artificial nests and guarantee the viability of the targeted species creates a
340 conservation trap (Cardador et al., 2015).

341 The estimated cost to accommodate all Roller and Lesser Kestrel breeding pairs in artificial
342 nests within the Castro Verde SPA is 4500€/year, considering the occupation rates of breeding
343 walls and towers, wooden nest-boxes and clay pots. Although other solutions (e.g. providing
344 only wooden nest-boxes or clay pots) could be slightly cheaper (Table 1 and Figure A1),
345 previous studies carried out in the area showed that these nests can reach very high
346 temperatures during hot days, leading to chick physiological stress and mortality (Catry et al.,
347 2011a; 2015).

348 Whilst the recovery of both populations through nest-site provisioning was funded by
349 government budgets, their future conservation may be jeopardized by the unsustainable need
350 to perpetuate the implementation of conservation actions as well as by the lack of funds
351 available to continue protecting both species. The recent down listing of Lesser Kestrels and
352 Rollers to "Least Concern" may have thus been a hasty decision because both species still
353 require continued conservation management and funding, even if their populations are no
354 longer threatened according to IUCN criteria.

355 **4.3 Funding conservation-reliant species: the potential of tourism revenues** 356 **for conservation**

357

358 Government budgets remains the central funding source for conservation, especially in
359 protected areas (Emerton et al., 2006; Mansourian & Dudley, 2008; Steven et al., 2013). Major
360 conservation budgets concentrate on funding nature-friendly management practices (e.g.
361 through Agri-Environmental Schemes or Paying for Ecosystem Services Schemes; Batáry et
362 al., 2015; Chakrabarti et al., 2019), or on species-specific recovery action plans that are based
363 on a short-term response to an identified emergency threat, and usually fail to evaluate long-
364 term threats that may persist once funding ends (Scott et al., 2010). In the Castro Verde SPA,
365 the provisioning of new structures for cavity nesting birds is a specific measure funded through
366 Agri-Environmental Schemes (AESs), part of the Rural Development Programme (RDP).
367 However, this voluntary measure had no engagement by farmers and no new nest-sites were
368 provided under this scheme (authors' personal observation).

369 Nature-based tourism has been increasingly seen as an opportunity to supplement government
370 budget allocations (Steven et al., 2013), having the potential to generate enough local income
371 to reduce the need for long-term external financing for conservation (albeit not entirely, Kiss,
372 2004). Birdwatching is a significant and expanding subsector of the tourism industry, where
373 people travel to see particular bird species or areas with high endemism or diversity (Steven et
374 al., 2013). Although it is hard to quantify the exact contribution of nature-based tourism to total
375 tourism revenues, the increasing attention to the high natural value of the region remains
376 unquestionable. The number of visitors to the Environment Education Centre of the LPN at
377 Castro Verde (a national environmental NGO) increased by 300% from 2005 to 2018, as well
378 as the supply of birdwatching tour guides (LPN, personal communication). The recent
379 classification of the municipality as UNESCO Biosphere Reserve, highlighting Castro Verde
380 as one of the last refuge for many globally threatened farmland birds in western Europe (Lesser
381 Kestrels, Rollers, Little and Great Bustards, Black-bellied Sandgrouse, Iberian Imperial Eagle),
382 has certainly played a fundamental role in raising tourism revenues. The 4500€ required to fund
383 the provisioning of nest-sites represents only 0.6% of the total income from lodging visitors in
384 2017 and highlights the great potential of using local tourism revenues to fund the conservation
385 of threatened species in the area.

386 Tourism and conservation can mutually support each other, especially when recognizing the
387 rich and varied ecosystems services provided by many species (Czajkowski et al., 2014; Kiss,
388 2004; Steven et al., 2013; Wei et al., 2018). For example, in Poland “stork villages” generate
389 substantial income to local communities while supporting tourism management and improving
390 public environmental awareness (Czajkowski et al., 2014). On a much larger scale, the
391 conservation of Giant Pandas *Ailuropoda melanoleuca* in China generates 10 to 27 times the
392 cost of maintaining key habitats in reserves (Wei et al., 2018). The values presented in our
393 study demonstrate the substantial economic benefits generated by bird and nature-related
394 tourism in the study region. The Convention on Biological Diversity (CBD) has already
395 provided guidelines for parties and other stakeholders to manage tourism activities in an
396 ecological, economic and socially sustainable manner (CBD, 2007).

397 In the most likely scenario in which the maintenance of Lesser Kestrels and Roller populations
398 will require long-term management investments, finding ways to foster self-sustainable
399 conservation is important to guarantee the viability of targeted populations in a foreseeable
400 future. Human-made structures have been opportunistically used for nesting by bird species
401 throughout the globe (Mainwaring, 2015). In the Castro Verde SPA, first known settlers of
402 Lesser Kestrels and Rollers, and still over 30% of the current population, nested in traditional
403 human buildings, with no records of birds breeding in their original natural nests (burrows in
404 cliffs or trees). Considering the nature-friendly reputation of the area and the income generated
405 by tourism, it should be possible for the council to require that all new buildings should include

406 cavities with the right dimensions for different cavity nesting species, a measure than should
407 be included in the council building regulations.

408 The conservation implications presented here are not limited to the Portuguese populations of
409 Lesser Kestrels and Rollers or even to bird species. Similar conservation challenges are likely
410 widespread amongst other cavity nesting species from different taxa, whose populations have
411 been recovered through the provisioning of nests following shortage of natural nest-sites (e.g.
412 seabirds: Bolton et al., 2004; marsupials: Beyer & Goldingay, 2006; bats: Mering & Chambers,
413 2014). Local conservationists and researchers need to consider the long-term consequences of
414 reactive conservation measures and search for solutions to secure the funding required to
415 guarantee the success of these measures, as well as the viability of target populations.

416

417

418 **5. Conclusion**

419 In the future, conservation reliance is likely to become even more pervasive because human
420 activities are driving more and more species towards extinction (Scott et al., 2010). This is the
421 case for many species, such as Lesser Kestrels and Rollers, that adapted to live in human
422 dominated landscapes and their persistence depends on the continuation of measures that
423 promote breeding and foraging habitats. Conserving global biodiversity is a great challenge,
424 and the budget needed to support it is likely to grow exponentially as the ranks of conservation-
425 reliant species increases. Here we provide evidence that nature-based tourism has the potential
426 to generate enough income to create self-sustainable conservation. But only by including a
427 broader spectrum of society, involving public participation and political commitment (James
428 et al., 2001; Scott et al., 2010), can tourism revenues be translated into effective conservation
429 measures and foster the long-term viability of wildlife populations.

430

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444

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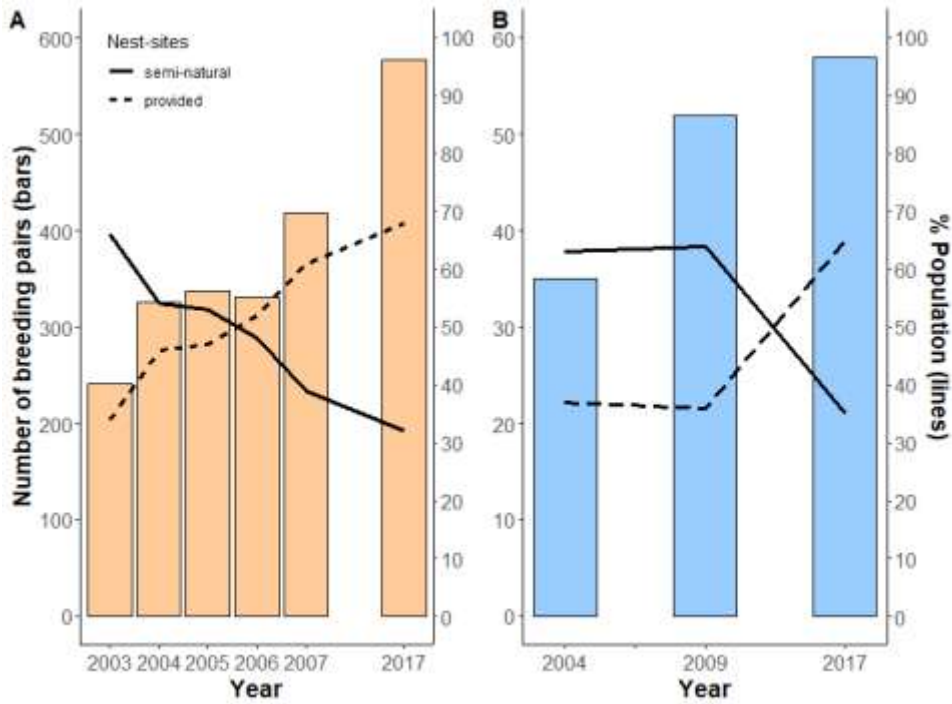
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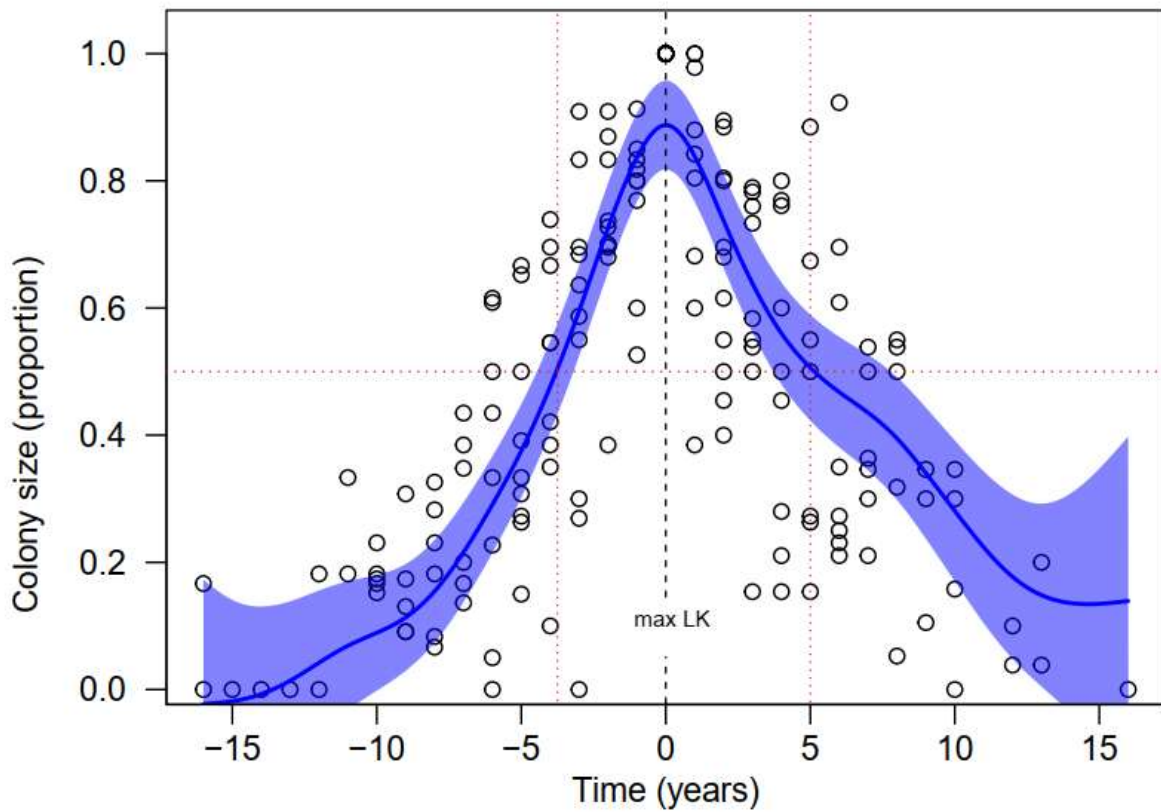
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695 *Figure 1: Population trends (bars) of (A) lesser kestrels and (B) European Rollers in the Castro Verde SPA, south*
 696 *Portugal (bars), and proportion of pairs occupying semi-natural (solid line) and artificial (dashed line)*
 697 *nest-sites. Presented values show minimum survey estimates.*

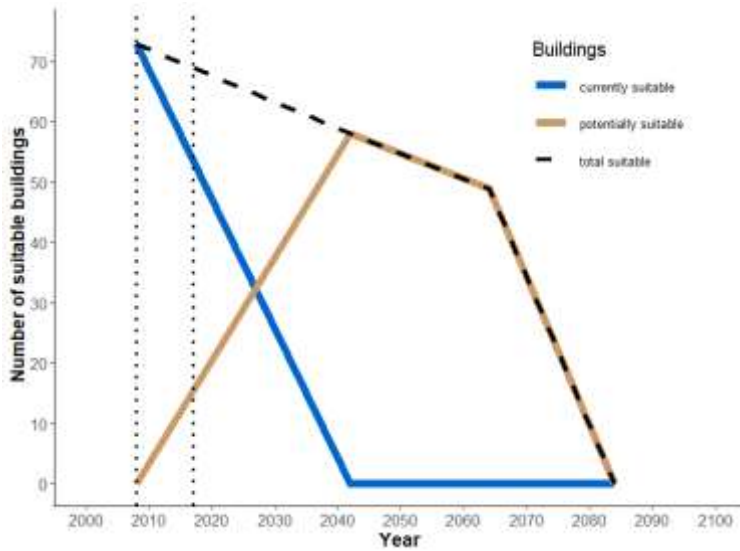
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699

700 *Figure 2: Temporal changes in size of lesser kestrel colonies (n=14) established on traditional adobe-made*
 701 *buildings. The trend line was estimated using a smoothing-spline mixed-effect model (loess) selected according*
 702 *to the AIC. Shaded area represents 95% confidence intervals. Dots represent colony size in relation to its*
 703 *maximum (year 0, max LK). The vertical lighter lines encompass the period when colonies were within the 50%*
 704 *of their maximum size. Results suggest the average longevity of a Lesser Kestrel colony in traditional buildings*
 705 *is less than 30 years.*

706



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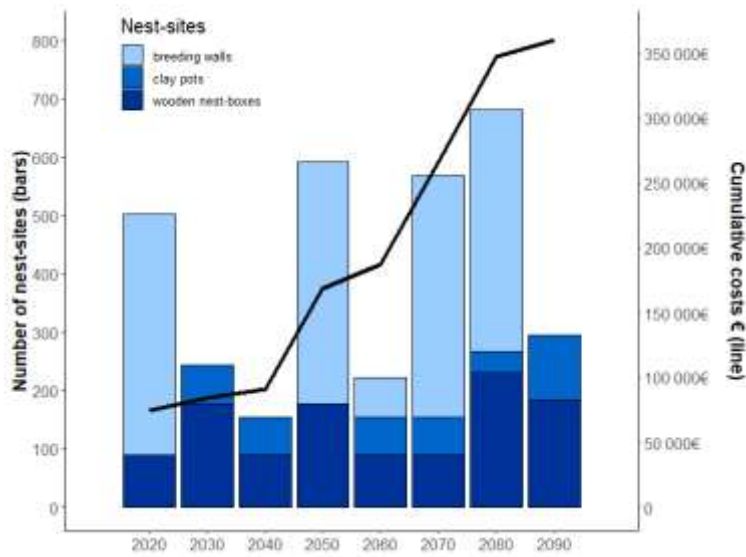
709 *Figure 3. Projected changes in the availability of traditional adobe buildings, suitable for breeding Lesser*
 710 *Kestrels and Rollers, during the next hundred years. Potentially suitable (those currently unsuitable but likely to*
 711 *become suitable due to natural degradation after abandonment) are predicted to increase at first but the gradual*
 712 *collapse of all structures will lead to the disappearance of all semi-natural nest-sites before 2100. Projections*
 713 *are based on the observed rate of change of 175 buildings between 2008 and 2017 (between dotted vertical lines).*

714

715

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718

719 *Figure 4: Conservation costs by decade (columns) and cumulative (black line) to sustain the current populations*
720 *of Lesser Kestrels and European Rollers in the Castro Verde SPA, southern Portugal. Estimates by decade*
721 *account for the replacement of provided artificial nest-sites at the end of its lifespan and new nests to*
722 *accommodate all breeding pairs currently using semi-natural nests.*

723

724 *Table 1: Characteristics of artificial nest-sites provided in the Castro Verde SPA and estimated costs per breeding*
 725 *pair. The occupation rate was calculated based on the survey conducted in 2017.*

726

Lesser Kestrel + Rollers	Number of nest-sites	Average Occupation rate 2017	Longevity (years)	Production costs (€)	Average cost/pair ± CI (€)
Breeding walls	69 (average)	0.44 ± 0.10	50	12 000	8.6 ± 1.7
Clay pots	1	0.73 ± 0.18	15	65	6.2 ± 1.7
Wooden nest-boxes	1	0.52 ± 0.19	7	30	7.3 ± 1.7
Rollers					
Isolated nest-boxes	1	0.44	7	30	10.95 (7.31 – 19.25)

727

728

729 *Table 2: Growth rate of tourism (2001-2017) and lodging income (2017) for the Castro Verde municipality, the*
 730 *South Alentejo region (including Castro Verde) and mainland Portugal.*

731

Region	Growth rate 2001-2017 (%)			Lodging income 2017 (thousand €)
	Number guests	Number nights	Lodging income	
Castro Verde	524.6	360.5	572.9	794
South Alentejo	248.8	254.8	338.9	13 201
Portugal	155.0	94.8	184.9	2 737 998

732 **Appendix 1**

733 In order to define what a suitable building was, we performed a binomial logistic
734 regression for the presence/absence of each species in buildings with at least one
735 available nest-site. We excluded isolated nest-boxes in trees or electric poles for
736 the Lesser Kestrel model as they only very seldomly nest in these. Therefore, total
737 sample size was 141 and 153 (out of the 412) buildings for the Lesser Kestrel and
738 the Roller model, respectively. Explanatory variables for the Lesser Kestrel
739 model were: human use, type of wall, type of roof, surrounding habitat, total
740 number of available nest-sites, total number of available nest-sites, distance to
741 nearest Lesser Kestrel colony (in meters), size of nearest Lesser Kestrel colony
742 (number of breeding pairs), and number of species of other cavity-nesting birds.
743 For the Roller models, we added distance to nearest structure with Rollers and
744 number of Roller pairs in that structure, and removed type of roof, as Rollers do
745 not nest under tiles. Variables were evaluated by model averaging using a subset
746 based on a variation in Akaike Information Criterion by less than 2 units
747 ($\Delta AIC < 2$) and looking at the p-values of full models and at the lower and higher
748 confidence bounds of each variable estimate.

749 The total number of available nest-sites in a structure was the only variable that
750 positively influenced the occupancy of a structure by both Lesser Kestrels and
751 Rollers and had the highest relative importance in both models (tables A1 and
752 A2). Suitable habitat was only positively selected by Lesser Kestrels, while
753 isolated nest-boxes were selected by Rollers. All other variables, including
754 different types of wall material and different degrees of human use, did not
755 influence the probability of a structure being occupied by either species. We thus
756 define a suitable structure as a structure with at least one available nest-site.

757

758 *Table A1: Lesser Kestrel full-model averaging using a subset of $\Delta AIC < 2$. Variables are ranked according to their*
 759 *relative importance (proportion of the number of times they appeared in the model. Relevant variables were the*
 760 *ones where confidence intervals (CI) did not include 0 (zero).*

Lesser Kestrel model			
Variable	Estimate	CI	Relative importance
Total number of available nest-sites	0.15	0.06 - 0.25	1.00
Suitable habitat	2.22	0.55 - 3.99	0.98
Distance to nearest Lesser Kestrel colony	0.00	0.00 - 0.00	0.84
Roof: Arabic tiles	-0.21	-1.68 - 1.04	0.64
Roof: no roof	-1.24	-3.90 - 0.02	
Size of nearest Lesser Kestrel colony	0.00	-0.04 - 0.03	0.26
Wall: adobe walls	-0.21	-3.35 - 0.99	0.18
Wall: stone walls	-0.16	-4.44 - 2.68	
Human use: abandoned	-0.03	-2.54 - 1.52	0.06
Human use: sporadic use	-0.01	-2.04 - 1.68	
Human use: intensive use	-0.04	-2.90 - 1.49	
Intercept	-2.26	-4.78 - 0.26	

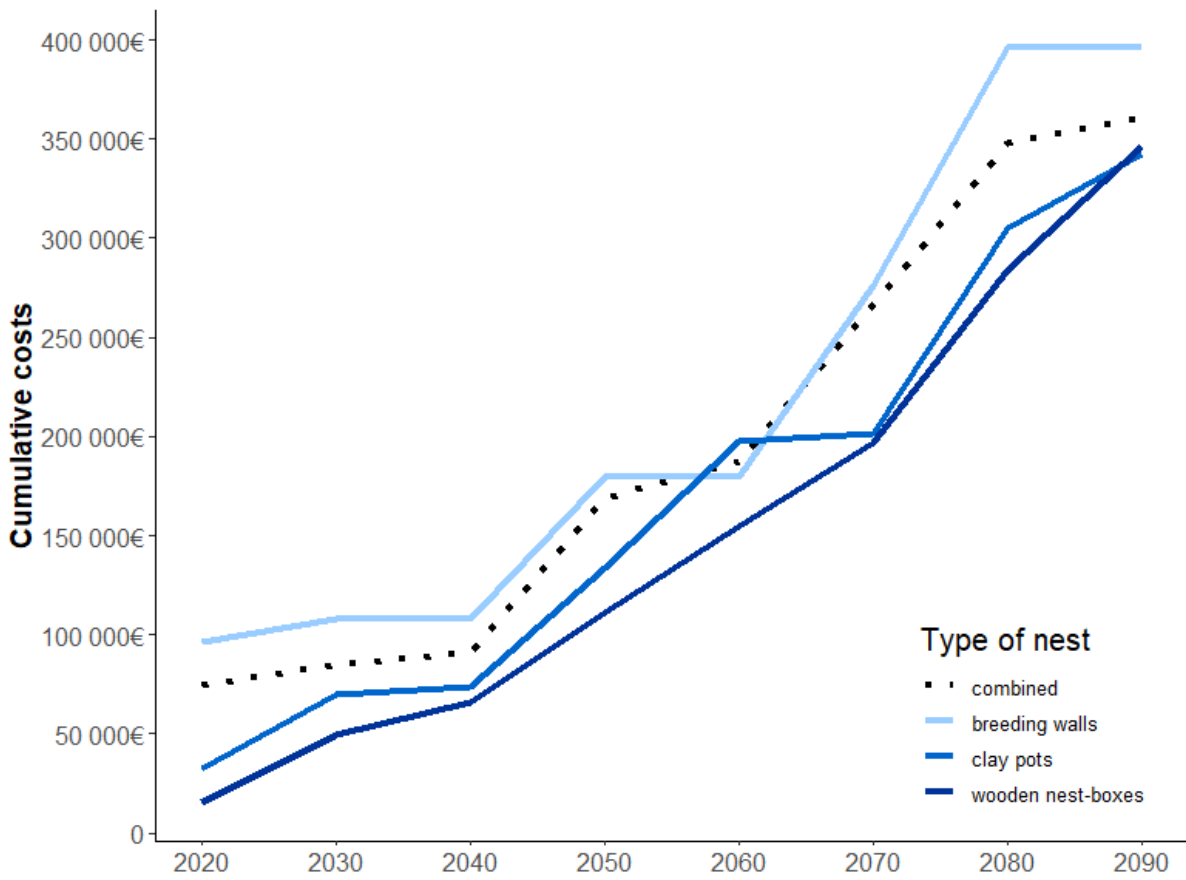
761

762 *Table A2: Roller full-model averaging using a subset of $\Delta AIC < 2$. Variables are ranked according to their relative*
 763 *importance (proportion of the number of times they appeared in the model. Relevant variables were the ones*
 764 *where confidence intervals (CI) did not include 0 (zero).*

Roller model			
Variable	Estimate	CI	Relative importance
Total number of available nest sites	0.17	0.05 - 0.29	1.00
Suitable habitat	18.01	-3019.14 - 3055.58	0.99
Wall: adobe wall	3.27	-0.49 - 7.29	0.96
Wall: isolated nest-boxes	5.31	1.23 - 9.88	
Wall: stone wall	3.77	-0.79 - 8.61	
Number of Roller pairs in nearest structure with Rollers	-0.27	-1.44 - 0.28	0.46
Distance to nearest Lesser Kestrel colony	0.00	0.00 - 0.00	0.38
Size of nearest Lesser Kestrel colony	0.00	-0.02 - 0.05	0.32
Distance to nearest Roller	0.00	0.00 - 0.00	0.30
Human use: abandoned	-0.08	-3.16 - 1.24	0.08
Human use: sporadic use	-0.06	-2.90 - 1.35	
Human use: intensive use	0.00	-2.35 - 2.38	
Intercept	-22.37	-3041.70 - 2996.95	

765

766 **Appendix 2**



767

768 *Figure A1: Cumulative conservation costs to sustain the current populations of Lesser Kestrels and European*
769 *Rollers in the Castro Verde SPA, southern Portugal. Different scenarios, considering the provisioning of only*
770 *one type of artificial nest-sites (solid lines) and combining the three types (dotted line, the original provided in*
771 *the main manuscript) are shown for comparison. Estimates by decade account for the replacement of provided*
772 *artificial nest-sites at the end of its lifespan and new nests to accommodate all breeding pairs currently using*
773 *semi-natural nests.*

774

775 **Appendix 3**

776 *Table A3: Percentage of the Lesser Kestrel and Roller populations of the Castro Verde SPA in each type of nest*
 777 *(2017).*

Type of nest		Lesser Kestrels (%)	European Rollers (%)
Semi-natural	Under tiles	12	0
	Semi-natural cavities	20	33
Artificial	Plastered walls	19	12
	Breeding walls/towers	36	22
	Clay pots	7	10
	Wooden nest-boxes	6	22

778