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Density-dependent productivity in a colonial vulture at two spatial scales

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Running head: Multi-scale density dependence

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24 ABSTRACT. Understanding how density dependence modifies demographic parameters
25 in long-lived vertebrates is a challenge for ecologists. Two alternative hypotheses have
26 been used to explain the mechanisms behind density-dependent effects on breeding
27 output: habitat heterogeneity and individual adjustment (also known as interference
28 competition). A number of studies have highlighted the importance of habitat
29 heterogeneity in density dependence in territorial species, but less information exists on
30 demographic processes in colonial species. For these, we expect density-dependent
31 mechanisms to operate at two spatial scales: colony and breeding unit. In this study we
32 used long-term data from a recovering population of Cinereous Vultures (*Aegypius*
33 *monachus*) in southern Spain. We analyzed a long-term data set with information on
34 2162 breeding attempts at four colonies over a nine year period (2002-2010) to evaluate
35 environmental and population parameters influencing breeding output. Our results
36 suggest that breeding productivity is subject to density-dependent processes at the
37 colony and the nest site scale and is best explained by interference competition. Factors
38 intrinsic to each colony, as well as environmental constraints linked to physiography
39 and human presence, also play a role in regulatory processes. We detected the existence
40 of a trade-off between the disadvantages of nesting too close to conspecifics and the
41 benefits of coloniality. These could be mediated by the agonistic interactions between
42 breeding pairs and the benefits derived from social sharing of information by breeding
43 individuals. We propose that this trade-off may play a role in defining colony structure
44 and may hold true for other colonial breeding bird species. Our findings also have
45 important management implications for the conservation of this threatened species.

46

47 *Keywords: Aegypius monachus, breeding success, Cinereous Vulture, coloniality,*
48 *density dependence, habitat heterogeneity, interference competition, population*
49 *regulation, productivity.*

INTRODUCTION

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51

52 Understanding the processes shaping and regulating the dynamics and size of animal
53 populations has been an on-going pursuit of ecology (Caughley 1994, Hixon et al.
54 2002). Density dependence is one of the issues attracting most attention from ecologists,
55 due to the key role it plays in modeling breeding rates and survival across a range of
56 taxa including plant, invertebrate and vertebrate species (Goldberg et al. 2001, Sergio
57 and Newton 2003, Boggs and Inouye 2012). Two hypotheses have been invoked to
58 explain the mechanisms behind density-dependent breeding output: the habitat
59 heterogeneity hypothesis (HHH) and the individual adjustment hypothesis (IAH, also
60 referred to as interference competition) (see Grünkorn et al. 2014). The HHH propounds
61 that increasing breeding densities lead to the saturation of optimal breeding sites. New
62 breeding units are then forced to occupy inferior quality habitats where breeding output
63 is lower. While this does not reduce the breeding rate of all pairs, it does increase the
64 proportion of low quality sites with lower breeding output (Sergio and Newton 2003).
65 On the other hand, the IAH suggests that increasing densities lead to higher frequencies
66 of agonistic conspecific interactions and competition between breeding units. A key
67 difference is that this process affects all individuals equally, resulting in reductions in
68 the breeding rates of all pairs (Sillett et al. 2004).

69

70 Growing evidence suggests that the HHH adequately explains density-dependent
71 breeding output in territorial species (Gaillard et al. 1993, Coltman et al. 1999, Carrete
72 et al. 2006, Krüger et al. 2012). However, information on colonial species is limited and
73 has focused mainly on seabirds (Ashbrook et al. 2010, Szostek et al. 2014, Oppel et al.
74 2015). Some studies suggest that the IAH may play a preponderant role in these species:
75 in growing colonies breeding rates may be affected by increased competition for food

76 resources in foraging areas (Fernández et al. 1998, Tella et al. 2001) or by increased
77 conspecific interactions in breeding areas (e.g. agonistic interactions at nest sites
78 between breeding pairs) (Bretagnolle et al. 2008). However, in colonial species these
79 mechanisms may operate at different spatial scales, complicating the detection of
80 density dependence. Interactions between conspecifics may occur between specific
81 breeding units within a colony (e.g. at the nest or burrow) or between all individuals of
82 the colony (e.g. in overlapping foraging areas). Thus, density dependence may occur at
83 the breeding unit scale, at the colony scale or at both scales simultaneously. In this
84 context, multi-scale approaches evaluating the factors relevant at each scale enable
85 detection of these processes and allow for a comprehensive understanding of their
86 underlying causes (Ray and Hastings 1996, Rogers and Schindler 2011).

87

88 Here we study the effects of density dependence on long-term breeding output in a
89 semi-colonial avian scavenger at two spatial scales: colony and nest site. Our study
90 model was the Cinereous Vulture (*Aegypius monachus*), a globally near threatened
91 species (BirdLife International 2015) which breeds in loose colonies. Data covered a
92 nine-year period of a monitoring program at four Cinereous Vulture colonies in
93 Andalusia (southern Spain) where the population has been protected for four decades.
94 This protection has led to a significant decline in human interference and substantial
95 demographic growth (Dobado et al. 2012), providing a unique opportunity to study
96 natural demographic processes, as human-related factors were no longer expected to be
97 the main driving force of population trends.

98

99 We aimed to determine the response of Cinereous Vulture breeding productivity to
100 changes in conspecific densities at both the colony and nest site scale. We also assessed

101 the relative contribution of environmental factors highlighted as important by previous
102 research. Firstly, at the colony scale, a common prediction arises for the IAH and HHH:
103 long-term changes in productivity will be driven by variations in density of
104 conspecifics. Proximate factors would be linked to saturation of potential breeding sites
105 within the colony or to changes in colony structure and relative position of nests.
106 Secondly, at the nest site scale we expect that if the IAH is operating, nests located close
107 to each other (i.e. with higher rates of conspecific interactions) will experience reduced
108 breeding success. Also, according to the IAH, we expect that newly-established
109 breeding pairs will have similar productivity to older breeding units (as nest site habitat
110 would not play a role in influencing fecundity). Conversely, under the HHH we would
111 expect nest site habitat, and not proximity to neighbors, to determine changes in
112 productivity.

113

114 METHODS

115

116 *Study species and area.*

117

118 The Cinereous Vulture is a large avian scavenger whose colonies may hold up to
119 hundreds of pairs, with nests separated by distances ranging from a few meters to
120 several kilometers (Cramp and Simmons 1980, Dobado et al. 2012). Monogamous pairs
121 build a nest on the top of large trees (usually oaks or conifers) in areas with low human
122 presence (Donázar et al. 2002, Margalida et al. 2011). A single egg is laid and the chick
123 fledges after 50-60 days of incubation and 120 days of development (Cramp and
124 Simmons 1980). The species is found from the Iberian Peninsula to central Asia and has

125 gone extinct or suffers on-going declines in many parts of its range (BirdLife
126 International 2015).

127

128 Our study was conducted in Andalusia, southern Spain, where, throughout the study
129 period 200-300 pairs bred in four distinct colonies in the Sierra Morena mountain range:
130 Sierra Pelada, Sierra Norte, Sierra de Hornachuelos and Sierra de Andújar (hereafter
131 referred to as S. Pelada, S. Norte, S. Hornachuelos and S. Andújar) (see Fig. 1).

132 Colonies occupy areas ranging from 200 to 750m above sea level where climate is
133 semi-continental Mediterranean (Donázar et al. 2002). Vegetation cover is a matrix of
134 forested areas (mainly evergreen oaks) and dehesa-type habitats (open landscapes
135 dominated by Mediterranean scrubland with scattered woodland patches and isolated
136 trees). The westernmost colony (S. Pelada, see Fig. 1) has been transformed since the
137 1950's for forestry exploitation purposes: up to 70% of the colony is covered by
138 plantations of eucalyptus (*Eucalyptus sp.*), stone pines (*Pinus pinea*) and maritime pines
139 (*P. pinaster*) (Donázar et al. 2002). Currently, all Cinereous Vulture nest sites in
140 Andalusia lie within protected lands (82%) or within less than five km from the nearest
141 protected area (18%). Although human disturbance and persecution were considered an
142 important cause of nest failure in the past (Donázar et al. 2002, Dobado et al. 2012),
143 public education and protection of breeding areas has contributed to diminishing the
144 influence of these factors on the Andalusian population (Dobado et al. 2012).

145

146 *Field procedures and data collection.*

147

148 From 2002 to 2010, Cinereous Vulture colonies were monitored during the breeding
149 season between December and August. In the early part of the season (December to

150 April), monthly visits were made to check for occupation of previously known sites and
151 to locate new sites by observing courting behavior of adult birds. Tree nest species and
152 a GPS location was recorded for all nests located. Active nests were monitored for the
153 remainder of the season (May to August) with visits every two weeks to determine
154 breeding outcome. Observations were carried out with 60x telescopes at distances >300
155 m to avoid disturbing breeding birds.

156

157 For the purposes of this study, nesting attempts were classified as *successful* (fledging
158 confirmed) or *failed* (all nests where pairs were observed in attendance but which failed
159 to fledge a chick). Cinereous vultures bred on 726 different nest platforms between
160 2002 and 2010: S. Pelada (n = 263), S. Norte (n = 127), S. Hornachuelos (n = 134) and
161 S. Andújar (n = 202). Reuse of nest sites by breeding pairs during the study period
162 resulted in a dataset with information on 2162 breeding attempts.

163

164 *Variable selection.*

165

166 Nest sites were mapped using ArcGIS 10 software (ESRI), in combination with
167 Geospatial Modeling Environment (www.spataleecology.com/gme) and DEM Surface
168 Tools (www.jennessent.com) to determine values for physiography, vegetation, human
169 disturbance and population explanatory variables (see Table 1 and Appendix, Tables A1
170 and A2). For calculation of nest site variables, a 500m radius buffer around each nest
171 platform was defined as the area of influence on the nest (Margalida et al. 2011). An
172 initial selection of explanatory variables was made based on current knowledge of
173 Cinereous Vulture breeding requirements (weather, physiography, land use, and human
174 disturbance) and evaluators of breeding density (Cramp and Simmons 1980, Donázar et

175 al. 2002, Carrete et al. 2007, Dobado et al. 2012, Moreno-Opo et al. 2013, Guerrero-
176 Casado et al. 2013). In order to avoid co-linearity and non-independence of variables,
177 Spearman correlation coefficients were calculated for all variable pairs; those with
178 values of $|r| > 0.7$ were considered redundant and one of the variables was consequently
179 excluded from further analyses (Dormann et al. 2013) (see Table 1 for the final set of
180 variables used at both scales).

181

182 *Colony scale analyses: density-dependence*

183

184 Models were built firstly to test for differences in productivity between colonies and to
185 assess the importance of environmental factors. The best model of this set was then used
186 as a base model to evaluate the importance of different population parameters (see
187 Table 2). The response variable for all models at the colony scale was productivity per
188 colony and year (COLONY PRODUCTIVITY). This variable was calculated as the
189 proportion of successful nests to the total number of occupied nests (*successful* /
190 (*successful* + *failed*); values ranging between 0 and 1). The first set of models (colony
191 environment models, CE) included the explanatory variable COLONY fitted as a factor to
192 test for differences in productivity between the studied colonies (model CE1). A
193 variable reflecting yearly variations in weather which could influence Cinereous Vulture
194 productivity was also tested in this subset (model CE2) (RAIN; average daily rainfall
195 during the core period of the breeding season from February to July) (Donázar et al.
196 2002, Moreno-Opo et al. 2012). The following subset of models (colony density
197 dependence models, CD, in Table 2) was based on model CE3 and tested the existence
198 of density dependence by contrasting the importance of different population parameters.
199 Changes in colony productivity could be linked to increased saturation of potential

200 breeding sites within the colony (model CD1). This variable (SATURATION) was
201 calculated annually as the proportion of occupied nests to the maximum number of nests
202 recorded at the colony during the whole study period. Although this metric is similar to
203 the number of active nests in the colony (with which it is correlated), it has the
204 advantage of allowing comparison of densities between colonies which might differ in
205 carrying capacity. Finally, we tested the role of changes in colony structure and relative
206 position of nests (e.g. tighter packing of nests) (model CD2). To this end we used a
207 measure of the colony's social environment (COLONY SOCENV). This is based on an
208 individual nest index (NEST SOCENV) used to describe the relative position of each nest
209 within the spatial distribution of all other nests (Carrete et al. 2007). Values of NEST
210 SOCENV are negatively related to isolation (range 0-1, from more isolated to more
211 connected nests) and were defined by $NEST\ SOCENV_i = \sum \exp(-d_{ij})$; where $i \neq j$; d_{ij} is the
212 linear distance between nests i and j ; and j represents all active nests (see Carrete et al.
213 2007). COLONY SOCENV was calculated as the mean of all NEST SOCENV values in a
214 given year at each colony. Different values of COLONY SOCENV would therefore reflect
215 changes in colony structure which might in turn influence productivity.

216

217 *Nest site scale analyses: individual adjustment and habitat heterogeneity hypotheses*

218

219 Nest site scale analyses followed a similar approach to that used at the colony scale: we
220 contrasted models testing the relative importance of environmental factors described by
221 previous research as relevant at this scale, and used the best model obtained to construct
222 models testing our hypotheses on density dependence. The response variable was
223 productivity per nest and year (NEST PRODUCTIVITY); with a value of one for nests
224 where fledging was confirmed (*successful*) and a value of zero for all other occupied

225 nests (*failed*). Firstly we evaluated models containing habitat, physiography, and human
226 disturbance variables highlighted as important by previous research (see Table 1 for
227 description of variables, Table 2 for a list of the five lowest AIC nest environment
228 models tested, NE) (Donázar et al. 2002, Guerrero-Casado et al. 2013, Moreno-Opo et
229 al. 2012, 2013). As other non-evaluated factors could be involved in determining
230 productivity (Symonds and Moussalli 2011), we also included the colony in which a
231 nest was located (COLONY) as a factor.

232

233 As several nest environment models had similar AIC values ($\Delta AIC < 2$) (Burnham and
234 Anderson 2002), we selected the most parsimonious model fitted with only significant
235 variables (model NE5). Building on this model we tested density dependence to discern
236 between the IAH and the HHH. The IAH was evaluated by fitting variables which
237 would reflect interactions between nesting pairs (models ND1 and ND2). Thus, the
238 distance to the nearest active nest (NEIGHBOR) was used as a measure of direct agonistic
239 interactions between pairs (Stokes and Boersma 2000) whereas NEST SOCENV (see
240 above, Colony scale analyses) was used to reflect the relative position of each nest to all
241 other nests within the colony. The HHH was evaluated by assessing the potential
242 existence of differences in quality of nest sites (model ND3). If habitat heterogeneity
243 played an important role in our study population, we would expect new pairs to occupy
244 low quality sites while the best sites would be occupied by established pairs which had
245 bred in previous years. Although it was not possible to identify individual birds in our
246 study, Cinereous Vultures are known to reuse nest sites (Cramp and Simmons 1980),
247 allowing us to use the age of the nest as a proxy for potential variations in nesting
248 habitat quality (Sergio and Newton 2003). Therefore, we used the variable NEST AGE to
249 differentiate between new nests occupied by newly established pairs (which according

250 to the HHH would correspond to sub-optimal sites) and pre-existing nests built in
251 previous years occupied by older breeding units (high quality sites, according to the
252 HHH) (Cramp and Simmons 1980). Models with different combinations of these
253 variables were also contrasted (models ND4 – ND7).

254

255

256 *Modeling procedures*

257

258 Analyses were carried out by means of Generalized Linear Mixed Models (GLMM)
259 (Littell et al. 2006). Response variables were proportions (at the colony scale) and
260 binary (at the nest site scale), thus the appropriate error distribution was binomial (link
261 function: logit). To avoid non-independence of data, the nest site (at nest site scale) and
262 year (at both scales) were included as random terms. This allowed us to account for
263 effects associated to nest site (such as pair effects) and yearly fluctuations which could
264 otherwise not be measured. Missing values (n = 1 at colony scale; n = 233 at nest site
265 scale) were excluded in order to maintain constant sample size and enable model
266 comparison (Symonds and Moussalli 2011). Akaike's information criterion (AIC) at the
267 nest site scale and small-sample corrected AIC (AICc) at the colony scale were
268 calculated for all models. Model weights were calculated for each set (colony and nest
269 site scale) following Burnham and Anderson (2002). All statistical analyses were
270 performed with R 3.2.0 (R Core Team 2015).

271

272

RESULTS

273

274 Between 2002 and 2010, notable growth in breeding pair numbers was registered at
275 three of the four colonies (Fig. 1). S. Norte experienced the most dramatic population
276 increase (139%; $r_s = 0.972$, $P < 0.001$, $N = 9$), followed by S. Andújar (48%; $r_s = 0.861$,
277 $P = 0.001$, $n = 9$) and S. Pelada (36%; $r_s = 0.917$, $P < 0.001$, $n = 9$). In S. Hornachuelos,
278 changes in breeding pair numbers were not significant. Long-term significant changes
279 in productivity were only apparent in S. Pelada, where productivity decreased
280 throughout the study period ($r_s = -0.617$, $P = 0.077$, $n = 9$) ($P > 0.15$ in the three other
281 colonies).

282

283 At both scales models revealed that Cinereous Vulture productivity was associated with
284 variables measuring density-dependence. At the colony scale, the lowest AICc and most
285 parsimonious model (CD1, see Tables 2 and 3) showed productivity to be negatively
286 associated with SATURATION, indicating that colonies had lower breeding outputs in
287 years when the number of breeding pairs approached maximum occupation. Changes in
288 colony structure (COL SOCENV, model CD2 and CD3) were non-significant and did not
289 appear to affect productivity at the colony scale. At the nest site scale, the best model
290 was indicative of density-dependent processes by the IAH (model ND4, including
291 variables NEIGHBOR and NEST SOCENV, see Tables 2 and 3). Distance to the nearest
292 active nest (NEIGHBOR) was positively related to productivity, indicating that pairs
293 located at greater distances from another active nest were more likely to be successful.
294 On the other hand, the positive relationship between NEST SOCENV and productivity
295 suggests that nests which were ‘better connected’ to all other nests in the colony had
296 higher productivity values. These results reveal a trade-off between two counteracting
297 pressures: distance to the nearest active nest and relative position within the colony
298 (Fig. 2). Although both variables influence productivity simultaneously, they do so

299 unequally; distance to the nearest neighbor has a greater effect on breeding output.

300 Summary and mean values for response and predictor variables can be found in the

301 Appendix (Tables A1 and A2).

302

303 At the nest site scale, environmental variables evaluating physiography, vegetation and
304 human disturbance also played a role in explaining variations in productivity.

305 Productivity was associated to the species of nest tree (TREE), with nests on conifer or
306 oak trees suffering reduced productivity compared to nests in other tree species.

307 Similarly, surrounding tree cover (DOMINANT) indicated no differences between nests
308 surrounded by oaks or by conifers, but higher productivity values for nests surrounded
309 by other tree species (mainly *Eucalyptus sp.* or deciduous species). In addition,

310 productivity was negatively related to RUGGEDNESS. This indicates that successful nests
311 were more likely to be found in less rugged terrain. Finally, nests located further from
312 tracks (TRACK), and thus subjected to lower disturbance levels, registered higher
313 productivity.

314

315 It is worth noting that at both scales, the variable COLONY was highly significant in
316 explaining productivity. This variable showed a recurrent pattern across all models: S.
317 Norte was consistently associated with very significantly lower breeding outputs. In the
318 three remaining colonies (S. Pelada, S. Hornachuelos and S. Andújar) productivity was
319 intermediate or high (with no significant or only marginally significant differences
320 between these colonies).

321

322

DISCUSSION

323

324 Our results show that density-dependent processes affect productivity in the Cinereous
325 Vulture at both scales analyzed and conforms to the IAH. At the colony scale, higher
326 SATURATION values resulted in a density-dependent decline in productivity. Interference
327 competition at this scale could be acting either by depletion of resources or by
328 generalized intra-specific agonistic encounters (Bretagnolle et al. 2008). Cinereous
329 vultures are central-place foragers, with individuals from the same colony foraging in
330 overlapping areas at large distances (>50 km) from nests (Carrete and Donazar 2005,
331 Dobado et al. 2012). An increase in colony breeding density would lead to higher
332 densities in foraging areas and potentially to higher levels of competition and depletion
333 of food resources. This effect has been described in seabird colonies (Ashmole's halo)
334 (Ashmole 1963, Wakefield et al. 2013, Oppel et al. 2015) but has also been observed in
335 colonial raptors (Bonal and Aparicio 2008). Limitation of food in foraging areas can
336 ultimately have detrimental effects on colony productivity (Tella et al. 2001, Forero et
337 al. 2002). On the other hand, as breeding pair numbers and colony density increase, so
338 does the frequency of interactions between nesting pairs (Bretagnolle et al. 2008).
339 Frequent agonistic interactions between breeding pairs could affect incubation, brooding
340 and feeding rates or stress levels of breeding birds, with negative consequences for
341 breeding output (Forero et al. 2006).

342

343 At the more localized nest site scale, best models clearly supported the IAH and did not
344 include factors indicative of the HHH. Two factors indicating interference competition
345 (NEIGHBOR and NEST SOCENV) were significant, while the factor NEST AGE, which
346 would indicate differences in nest site quality (and support the HHH), was non-
347 significant and did not appear in the best models. Small nearest neighbor distances
348 (NEIGHBOR) indicative of frequent agonistic interactions resulted in lower productivity

349 (supported by field observations of frequent aggressive interactions between pairs
350 nesting in close proximity (E. Luque, *pers. comm.*)). However, nests that were well
351 connected to the rest of the colony (high NEST SOCENV values) had higher breeding
352 output. Although these results may initially appear contradictory, these variables
353 measure different aspects of a nest's spatial ecology: nearest neighbor distance
354 (NEIGHBOR) serves as an indicator of frequency of agonistic interactions, while NEST
355 SOCENV measures the position of the nest within the colony, which may be associated
356 to benefits derived from individuals' access to public information regarding quality of
357 foraging areas (Danchin et al. 2004, Deygout et al. 2010, Wakefield et al. 2013). When
358 considered jointly, they suggest the existence of a trade-off between the costs and
359 benefits of nesting close to conspecifics (see Fig. 2). However, the slope associated to
360 each variable in Fig. 2 indicates that direct conspecific interference at nest sites is more
361 important as a driving force of productivity in this species (i.e. changes in the value of
362 distance to neighbor are linked to larger variations in productivity). Furthermore, the
363 effects of conspecific interference on productivity (particularly at short distances
364 between nests) may play a role in determining the loose colonial breeding structure of
365 Cinereous Vultures. The benefits of coloniality (such as shared information) would be
366 outweighed by the costs (agonistic interactions) for pairs nesting at close quarters,
367 resulting in colonies where nests are well spaced apart. We propose that this trade-off
368 may hold true for other loosely colonial or semi-colonial bird species. How these
369 selective pressures, along with other costs and benefits of coloniality (e.g. mate choice,
370 extra pair copulation, predator detection, group defense (Møller 1987, Danchin et al.
371 1998)) determine individual recruitment and fitness is a matter that deserves close
372 attention in future fine-scale research on the adaptive value of coloniality.

373

374 At both scales, an important source of variation in breeding output was associated with
375 the explanatory variable COLONY. These results suggest that factors which were not
376 assessed by our study and which vary between colonies were influencing productivity.
377 Closer inspection of the variation in productivity reveals that S. Norte had the lowest
378 productivity and that S. Pelada was the only colony to register a significant decrease in
379 productivity during the study period. Several factors which may act in combination
380 could be behind these trends. In these two colonies, large numbers of immature
381 cinereous and griffon vultures (*Gyps fulvus*) are present year-round (P. Dobado & E.
382 Luque, pers. comm., Dobado et al. 2012). The presence of non-breeding individuals can
383 play an important role in population productivity by increasing interference at nest sites
384 (Carrete et al. 2006, Bretagnolle et al. 2008) or competition for food resources as
385 floaters gain access to social information on foraging areas (Deygout et al. 2010).
386 Observations of frequent agonistic interactions between nesting pairs and immature
387 vagrants in S. Norte corroborate this interpretation (E. Luque, pers. comm.). In the case
388 of S. Pelada, the recorded decrease in productivity may also be influenced by on-going
389 forestry exploitation activities which, despite increased protection, exposes breeding
390 birds to relatively higher levels of disturbance than in other colonies (Donázar et al.
391 2002).

392

393 At the nest site scale productivity was also related to vegetation cover, physiography
394 and human disturbance factors. Both the nest tree (TREE) and dominant tree species
395 surrounding the nest (DOMINANT) had a significant effect on productivity. However,
396 previous work has shown that nest tree selection in Cinereous Vultures is not species-
397 specific but related to the size and structure of the tree and the surrounding vegetation
398 (Donázar et al. 2002, Moreno-Opo et al. 2012, 2013). In this study, only S. Pelada has

399 areas dominated by *Eucalyptus* and deciduous species, while tree cover in the other
400 three colonies is homogenously limited to oaks and conifers. This leads us to conclude
401 that the link between tree species and productivity may in fact be a spurious relationship
402 ascribable to the particular vegetation features within S. Pelada colony and the low
403 productivity registered there. Models also showed that nests located in terrain which is
404 not excessively rugged (RUGGEDNESS) were more likely to succeed in fledging young.
405 This is in line with findings from previous studies, and is probably related to the
406 species' flight requirements (Donázar et al. 2002, Moreno-Opo et al. 2012). It is
407 interesting to note that human disturbance (measured by the distance to the nearest
408 track, TRACK) is still a relevant factor affecting productivity in Andalusia, despite
409 increased protection and control of human activities in breeding areas for four decades
410 (Margalida et al. 2011, Dobado et al. 2012). Long-term persistence of evasive
411 behaviors, despite the disappearance of negative effects associated with human
412 presence, can be expected in a long-lived species and may help explain these findings
413 (Donázar et al. 2002, Parks et al. 2007, Linhart et al. 2012).

414

415 Our results reinforce the idea that density dependence in colonial bird species could be
416 mostly determined by interference competition (Fernández et al. 1998, Tella et al. 2001,
417 Bretagnolle et al. 2008). This may be explained by the relative homogeneity of nesting
418 habitat within colonies and by shared foraging areas, in comparison to the spatially
419 structured heterogeneity typical of territorial species. . Furthermore, as predation is a
420 minor issue for this species, colonies do not display the nest site quality gradient
421 reported for smaller colonial birds whose nests are more likely to be predated if they are
422 located in the colony periphery (Gilchrist 1999, Massaro et al. 2001). It follows from
423 this that the prevalence of density dependent demographic processes based on the HHH

424 or the IAH may be species-specific in relation to life-history strategies. This specificity
425 would be related not only to the species' coloniality, but also to other aspects such as
426 the degree of individual sociability (which may vary with age and thus affect spatial
427 segregation) and to the importance of public information in determining foraging
428 strategies. In this scenario, it is possible to envisage changes in productivity as the result
429 of a combination of both processes (HHH and IAH) (Grünkorn et al. 2014).

430

431 An important result from our research is the positive effect of connectivity (the nests'
432 social environment) on productivity. This finding highlights the adaptive value of
433 nesting near conspecifics. In this case the benefits would not be related to defense
434 against predators as occurs in small body-sized colonial birds (Serrano et al. 2005), but
435 perhaps to increased foraging efficiency as a consequence of shared information.
436 Similar patterns have been observed in other social vertebrates exploiting spatially and
437 temporally unpredictable resources (Wakefield et al. 2013, Cortés-Avizanda et al.
438 2014). This raises the question: could the advantages of connectivity between nests vary
439 with colony size? Optimal values of connectivity could be related to intermediate-sized
440 colonies: in small colonies foraging efficiency would be compromised, while in large
441 colonies the potential benefits of increased connectivity would be outweighed by
442 interference competition. Research on colonial species at a metapopulation scale will be
443 necessary to shed light on this aspect.

444

445 *Conclusions and conservation implications*

446

447 Overall, our study highlights the importance of multi-scale approaches and suggests that
448 productivity in colonial species may be affected by more factors than those reported by

449 previous studies. Our results reveal that the interaction between a nest's position within
450 the colony and its distance to the nearest neighbor lead to a trade-off between the
451 benefits (shared public information) and costs (agonistic interactions) of colonial
452 breeding. Nest productivity would thus be optimized at locations which minimize the
453 frequency of interactions with other pairs, while still remaining well positioned within
454 the colony to profit from access to public information. However, this relationship may
455 be confounded by other environmental factors that can impose strong spatial constraints
456 (e.g. nest tree availability, ruggedness). The presence and the abundance of non-
457 breeding conspecifics (Carrete et al. 2006), as well as the numbers of individuals of
458 competing scavenger species (griffon vultures in this case) may further obscure
459 regulatory processes. In conclusion, understanding density-dependent productivity goes
460 far beyond the simple examination of factors related to the proximity between
461 reproductive units. Multi-scale interactions between the study species and physical and
462 biological factors should also be considered. Discerning what variation in productivity
463 is ascribable to environmental factors and / or to individual breeding strategies may be a
464 major future challenge.

465

466 Our results also have relevant implications for the long-term conservation of this
467 endangered species. We highlight that for successful breeding, pairs require a large area
468 which allows the distance between nests to be maximized, while staying within a range
469 which permits pairs to benefit from colonial behavior. Consequently, long-term viable
470 Cinereous Vulture colonies would require huge areas of land meeting certain
471 requirements for hosting breeding pairs. Otherwise, nest site shrinkages may lead to
472 declines in breeding output and reduced population viability. How these needs fit with
473 changes to the European landscape in the next century (see Navarro and Pereira 2012,

474 Cortés-Avizanda et al 2015) should be a research priority, particularly as the
475 conservation strategy for large scavengers often involves the restoration of viable
476 metapopulations by means of costly conservation measures such as reintroductions
477 (Hirzel et al. 2004, Margalida et al. 2013).

478

479

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481

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496

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APPENDICES

686

687 APPENDIX A. Mean values of response and predictor variables used for analyses of

688 Cinereous Vulture productivity at colony and nest site scale.

689 **Table 1.** Response and explanatory variables used in analyses of Cinereous Vulture productivity at colony and nest site scales in Andalusia during
 690 the study period (2002-2010). Response variables are highlighted in bold. All values were calculated for each year of the study.

	Variable	Description and calculation	Data source
	COLONY PRODUCTIVITY	Colony productivity (n successful nests / (n failed + n successful nests)).	Fieldwork
COLONY SCALE	COLONY	Breeding colony.	Fieldwork
	RAIN	Average daily rainfall (mm) between February and July.	(IIFAP 2012)
	SATURATION	Percentage colony saturation (n nests / maximum n nests recorded during the study).	Fieldwork
	COLONY SOCENV	Colony social environment (average NEST SOCENV index, see below).	GIS
	NEST PRODUCTIVITY	Nest productivity (failed (0) or successful (1)).	Fieldwork
	<i>Vegetation</i>		
	TREE	Tree species on which the nest platform was built.	Fieldwork
	DOMINANT	Dominant tree species in 500m radius around the nest.	GIS, vegetation cover (SIOSE 2011)
	% CONOAK	Percentage cover of conifers and oaks in 500m radius around the nest.	GIS, vegetation cover (SIOSE 2011)
	% SHRUB	Percentage cover of shrubs in 500m radius around the nest.	GIS, vegetation cover (SIOSE 2011)
	<i>Physiography</i>		
NEST SITE SCALE	ELEVATION	Ground elevation at nest tree.	GIS, digital terrain model (IGN 2010)
	RUGGEDNESS	Terrain ruggedness (standard deviation of elevation in 500 m radius around the nest). ¹	GIS, digital terrain model (IGN 2010)
	ASPECT	Slope orientation at nest tree.	GIS, digital terrain model (IGN 2010)
	<i>Human disturbance</i>		
	TRACK	Logarithm of distance (m) to nearest track or road.	GIS, digital maps (ICA 2001, SCA 2009, IECA 2012)
	<i>Population parameters</i>		
	COLONY	Breeding colony.	Fieldwork
	NEIGHBOR	Logarithm of distance (m) to nearest active nest.	GIS
	NEST SOCENV	Nest social environment ($(i) = \sum \exp(-d_{ij})$; where $i \neq j$; d_{ij} is the linear distance between nests i and j ; and j represents all active nests). ²	GIS
	NEST AGE	Newly built nest site or pre-existing site from previous years.	Fieldwork

691 ¹ see White (2006).

692 ² see text (Colony scale analyses) and Carrete *et al.* (2007).

694 **Table 2.** Generalized linear mixed models developed to investigate density-dependent productivity in Cinereous Vultures in Andalusia during the
 695 study period (2002-2010). Model sets test environmental factors (CE models at the colony scale, NE models at the nest site scale), and population
 696 parameters indicative of density dependence (CD models at the colony scale, ND models at the nest site scale). At the nest site scale, only the five
 697 best environmental models (NE) are shown due to the large number of variables fitted. Following lowest AICc / AIC and model parsimony
 698 criteria, models selected in each set were CE3, CD1, NE5, and ND4. Significant factors ($P < 0.05$) are highlighted in bold.

Response variable	Random variables	Model	AICc / AIC	Δ AICc / Δ AIC	Model weights
COLONY PRODUCTIVITY	YEAR	CE1 COLONY	231.9	5.2	0.069
		CE2 RAIN	258.2	31.5	0.000
		CE3 COLONY + RAIN	226.7	0	0.931
		CD1 COLONY + RAIN + SATURATION	223.2	0.9	0.374
		CD2 COLONY + RAIN + COLONY SOCENV	227.7	5.4	0.039
		CD3 COLONY + RAIN + SATURATION + COLONY SOCENV	222.3	0	0.587
		NE1 COLONY + TREE + DOMINANT + %SHRUB + ELEVATION + RUGGEDNESS + TRACK	2413.9	0.8	0.215
NE2 COLONY + TREE + DOMINANT + %CONOAK + ELEVATION + RUGGEDNESS + TRACK	2415.1	2	0.117		
NE3 COLONY + TREE + DOMINANT + ELEVATION + RUGGEDNESS + TRACK	2413.1	0	0.320		
NE4 COLONY + TREE + DOMINANT + %SHRUB + RUGGEDNESS + TRACK	2414.7	1.6	0.144		
NE5 COLONY + TREE + DOMINANT + RUGGEDNESS + TRACK	2414.0	0.9	0.204		
NEST PRODUCTIVITY	YEAR, NEST SITE	ND1 COLONY + TREE + DOMINANT + RUGGEDNESS + TRACK + NEIGHBOR	2412.8	1.6	0.202
		ND2 COLONY + TREE + DOMINANT + RUGGEDNESS + TRACK + NEST SOCENV	2415.5	4.3	0.052
		ND3 COLONY + TREE + DOMINANT + RUGGEDNESS + TRACK + NEST AGE	2415.9	4.7	0.043
		ND4 COLONY + TREE + DOMINANT + RUGGEDNESS + TRACK + NEIGHBOR + NEST SOCENV	2411.2	0	0.448
		ND5 COLONY + TREE + DOMINANT + RUGGEDNESS + TRACK + NEIGHBOR + NEST AGE	2414.7	3.5	0.078
		ND6 COLONY + TREE + DOMINANT + RUGGEDNESS + TRACK + NEST SOCENV + NEST AGE	2417.4	6.2	0.020
		ND7 COLONY + TREE + DOMINANT + RUGGEDNESS + TRACK + NEIGHBOR + NEST SOCENV + NEST AGE	2413.3	2.1	0.157

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701 **Table 3.** Generalized linear mixed models selected to explain Cinereous Vulture productivity in relation to density dependence at colony and nest
 702 site scale in Andalusia during the study period (2002-2010). SP = S. Pelada; SN = S. Norte; SH = S. Hornachuelos; SA = S. Andújar.

Model	Response variable	Explanatory variables	Estimate	Standard error	Significance
Model CD1	COLONY PRODUCTIVITY	Intercept	1.206	0.369	
		COLONY	SA: 1.206	0.369	ns
		(SA ~ SP > SH >>> SN)	SP: -0.150	0.120	ns
			SH: -0.248	0.153	*
			SN: -0.911	0.154	***
Model ND4	NEST PRODUCTIVITY	RAIN	-0.060	0.099	ns
		SATURATION	-0.947	0.412	*
		Intercept	-0.621	1.011	
		COLONY	SA: -0.138	0.224	ns
		(SA ~ SH ~ SP >>> SN)	SP: -0.710	0.311	ns
			SH: -0.621	1.011	ns
			SN: -0.715	0.205	***
		TREE	Others: -0.621	1.011	ns
		(Others >> Quercus ~ Pinus)	Pinus: -1.291	0.713	*
			Quercus: -1.869	0.735	*
		DOMINANT	Others: -0.621	1.011	ns
		(Others >> Quercus ~ Pinus)	Pinus: -0.669	0.196	*
	Quercus: -0.628	0.267	*		
	RUGGEDNESS	-0.009	0.005	*	
	TRACK	0.498	0.154	**	
	NEIGHBOR	0.440	0.178	*	
	NEST SOCENV	3.977	2.105	*	

703 * $P < 0.05$; ** $P < 0.001$; *** $P < 0.0001$; ns = non-significant.

704 For relationship between categorical variables: “>” refers to significance of $P < 0.05$; “>>” to $P < 0.001$; “>>>” to $P < 0.0001$; “~” to non-significant differences.

FIGURES

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706

707 FIGURE 1. Iberian distribution of the Cinereous Vulture (after de la Puente et al. 2007) and
708 location of the four study colonies in Andalusia; productivity (black dots) and number of
709 breeding pairs (grey triangles) at each colony during the study period (2002-2010).

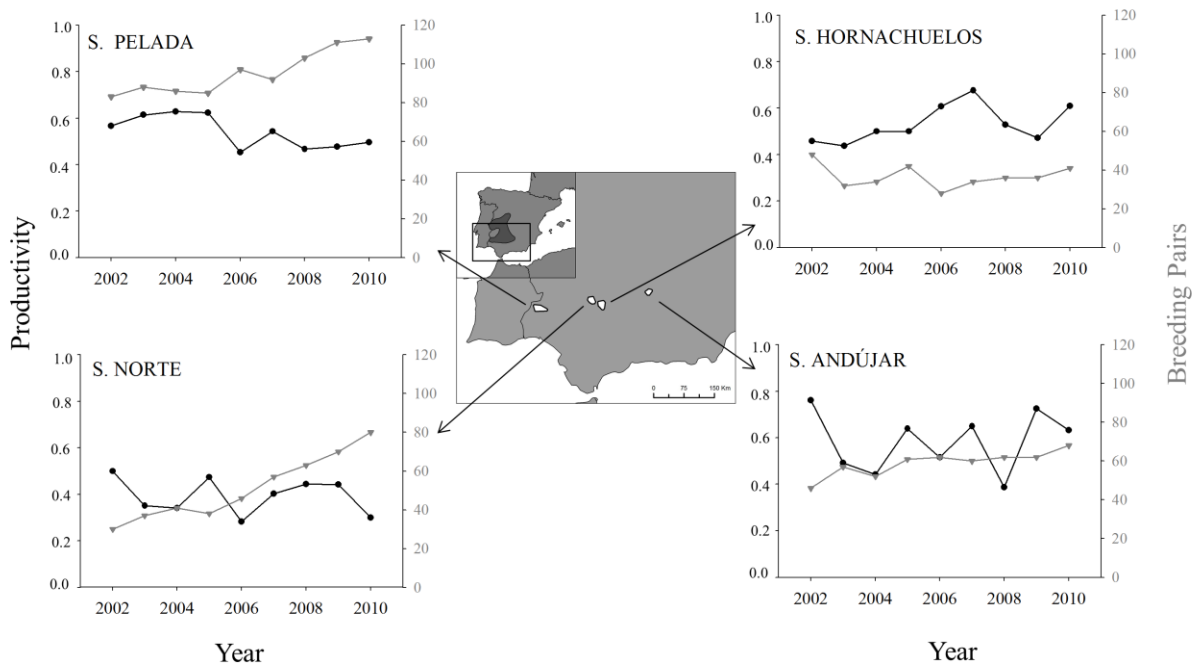
710

711 FIGURE 2. Graphical representation of the trade-off between distance to the nearest neighboring
712 nest (NEIGHBOR) and a nest's social environment (NEST SOCENV) and the effect of these
713 parameters on Cinereous Vulture nest productivity. The variable measuring the nest's social
714 environment ranges from zero to one (from lower to higher connectivity of a nest to all other
715 nests in the colony). This projection is based on model ND4 (nest site productivity, Table 2)
716 and uses default estimates from S. Pelada for all other fitted variables.

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718

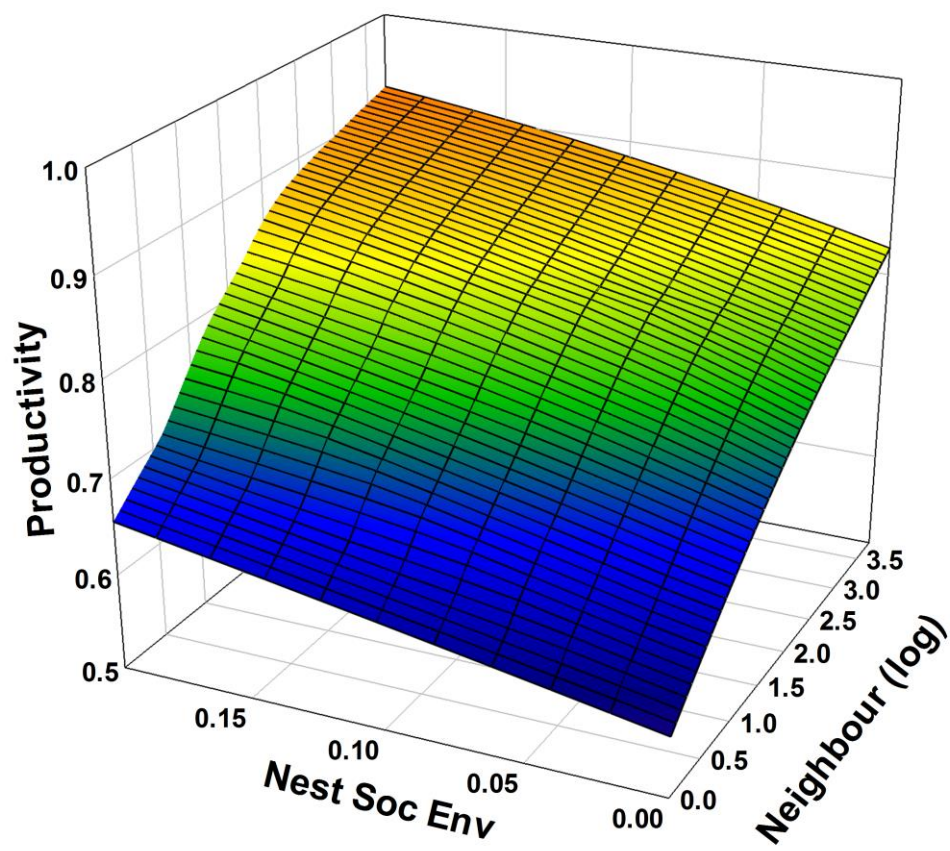
719 Figure 1.



720

721

722 Figure 2.



723