

1 **Vulture culture: dietary specialization of an obligate scavenger.**

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27 variation,

28 **Abstract**

29 Individual dietary variation has important ecological and evolutionary consequences.  
30 However, it has been overlooked in many taxa that are thought to have homogeneous diets.  
31 This is the case of vultures, considered merely as “carrion eaters”. Given their high degree  
32 of sociality, vultures are an outstanding model to investigate how inter-individual  
33 transmissible behaviors drive individual dietary variation. Here, we combine GPS-tracking  
34 and accelerometers with an exhaustive fieldwork campaign to identify the individual diet  
35 of 55 griffon vultures (*Gyps fulvus*) from two Spanish populations that partially overlap in  
36 their foraging areas. We found that individuals from the more humanized population  
37 consumed more anthropic resources (e.g., stabled livestock or rubbish), resulting in more  
38 homogeneous diets. In contrast, individuals from the wilder population consumed more  
39 wild ungulates, increasing their dietary variability. Between sexes, we found that males  
40 prefer anthropic resources more than females. Interestingly, in the shared foraging area,  
41 vultures retained the dietary preference of their original population, highlighting a strong  
42 cultural component of vulture foraging. Overall, these results expand the role of cultural  
43 traits in shaping key behaviors, and call for the need of including cultural traits in Optimal  
44 Foraging models, especially in those species that strongly rely on social information while  
45 foraging.

46 **Introduction**

47 Animal populations are composed of individuals that frequently differ in their ability to  
48 exploit resources, such as food. Although early ecologists had noted the occurrence of  
49 individual dietary variation or specialization [1], their eco-evolutionary consequences have  
50 not been recognized until more recently [2,3]. For instance, diet preferences make certain  
51 individuals more vulnerable to natural [2] and anthropogenic [4] hazards, ultimately  
52 leading to differential fitness [5]. Therefore, individual dietary specialization is an  
53 important component of natural selection that can even create reproductive isolation  
54 between individuals of the same population and facilitate adaptive speciation [2].

55 Causes of dietary specialization include factors related to both the environment  
56 (extrinsic) and the individual (intrinsic). First, extrinsic factors, such as prey attributes (e.g.,  
57 availability, energetic content, and predictability), can contribute to define individual  
58 dietary differences [2]. Notably, inter- and intraspecific competition may force subordinate  
59 or inexperienced individuals to consume suboptimal or secondary prey [6,7,8], especially  
60 where resources are scarce [9] thus enhancing inter-individual variation. Second,  
61 individual preferences can be driven by intrinsic factors associated with phenotypic traits  
62 such as body size, sex or social status [4,10,11]. In addition, some individuals are more  
63 cautious than others against predator and parasite risks associated with food [12], which  
64 may also determine different diets. Social facilitation processes may also result in different  
65 individual dietary patterns [13]. For instance, individuals may develop a preference for a  
66 particular diet either by imitating their parents during the juvenile stage or by imitating  
67 more experienced individuals while foraging in a particular area or on a particular resource.

68 Both extrinsic and intrinsic processes have been shown to be capable of generating cultural  
69 patterns with population-level effects in birds and mammals [14,15].

70 Traditionally, researchers have considered some species as non-specialized  
71 consumers because the resources they consume have been misinterpreted as homogenous.  
72 In this sense, vultures are usually considered as consumers of a typical prey type and size  
73 (e.g., ungulate carcasses in the case of *Gyps* vultures; [16]). This preconception assumes  
74 that all individuals in a vulture population have similar diets, which would be determined  
75 by the local availability of the different carrion resources (e.g., wild vs. domestic ungulates;  
76 [16,17,18] rather than by individual variation. However, this assumption is questioned by  
77 the growing body of evidence showing that carrion is a highly heterogeneous resource, not  
78 only in terms of abundance, but also of quality, predictability and risks associated to its  
79 consumption [19,20].

80 According to Optimal Foraging Theory, the net energy gain obtained during  
81 feeding is the difference between the energy ingested and the energy used in searching and  
82 handling the food [21]. In this scenario, vultures evolved to consume a resource that needs  
83 little manipulation but involves high searching cost, which they address via highly efficient  
84 foraging strategies [22,23]. Thus, vultures spend much time foraging, and rely heavily on  
85 social information obtained from conspecifics [24]. Social information transfer leads to  
86 two possible foraging scenarios: a) “local enhancement”, in which vultures feed on  
87 carcasses located by other individuals [25], and b) “cultural traits”, in which vultures learn  
88 to detect the most profitable carrion sources or food types from conspecifics [26]. The most  
89 straightforward prediction for both hypotheses is that individuals from the same population  
90 have similar diets. Given the long-distance movements of *Gyps* vultures [27,28], it is usual

91 for individuals from different populations to converge in an area far from their home  
92 colonies [28]. However, whether vultures in these shared areas are locally enhanced by  
93 vultures from other populations or retain the cultural traits of their own population is  
94 unknown. Thus, exploring the foraging behavior of vultures from different populations in  
95 shared and non-shared foraging areas may help to better understand the determinants of  
96 individual vulture foraging decisions.

97         Here, we combined radiotracking data from GPS and accelerometers and intensive  
98 field validation at the large spatial scale to address individual variation in the diet of griffon  
99 vultures (*Gyps fulvus*) from two Spanish populations that partially overlap in their foraging  
100 areas. We identified not only the diet of every tracked vulture, but also the specific sites  
101 where vultures ate, an aspect that has rarely been considered in intra-population diet  
102 studies. Our general hypothesis is that obligate scavengers may also exhibit individual  
103 dietary specialization, with social learning playing an important role in shaping individual  
104 vultures' diet. We expect to find lower variability in the diet of individuals inhabiting areas  
105 rich in predictable resources, such as intensive livestock farming, than in undisturbed sites.  
106 From previous ecological knowledge on griffon vultures, no clear prediction on how sex  
107 may influence individual diets can be delineated. Regarding social information, there are  
108 two alternative scenarios: 1) a “local enhancement” scenario, where individuals from  
109 different populations are expected to have similar diets when exploiting shared foraging  
110 areas (i.e., areas where these populations forage regularly), and 2) a “cultural trait”  
111 scenario, where individuals from different populations are expected to maintain the dietary  
112 preferences of their population of origin and have different diets even in the shared foraging  
113 area. Exploring the contribution of cultural traits in vulture diet at the individual level may

114 help to better understand the eco-evolutionary consequences of culture transmission in  
115 social species. Furthermore, it might be key to the conservation of vultures, which are  
116 globally threatened [29] and particularly vulnerable to anthropogenic hazards while  
117 foraging in human-dominated environments [30].

118

## 119 **Materials and Methods**

### 120 *Study species*

121 Griffon vultures are large scavengers weighting 6-11 kg. They are colonial cliff breeders  
122 with great flying capacities that allow them to forage over very large areas (up to 32,000  
123 km<sup>2</sup>; [28,31]). The diet of this vulture is mainly composed of carcasses of domestic and  
124 wild ungulates, with occasional contributions of smaller-sized vertebrates [16,32].

125

### 126 *GPS-tracking and study areas*

127 We captured 65 adult griffon vultures, 30 individuals in Southern Spain between December  
128 2014 and January 2015 and 35 individuals in Northern Spain between December 2015 and  
129 March 2016. The Southern area is a mountainous region (500-2,107 m a.s.l.) covered by  
130 Mediterranean woodlands and pasturelands, where the main human uses are traditional  
131 farming, hunting, forestry and tourism [33]. The Northern area is a flat area (28-659 m  
132 a.s.l.) surrounded by mid-sized mountains (up to 1500 m a.s.l.) and highly transformed for  
133 intensive agriculture, with traditional sheep livestock being replaced by intensive farming  
134 [34,35]. As a consequence, carrion sources in the Northern area are more predictable  
135 compared to the Southern one [36], although trophic resources can be considered abundant  
136 in both areas. In addition to these areas, both vulture populations share a second foraging

137 area in Southwestern Spain (Figures S1 and S2) where carrion from wild and domestic  
138 ungulates is also abundant [36].

139 We sexed vultures by molecular procedures [37], and determined age by  
140 morphological features [38]. All birds were equipped with 90 g GPS/GPRS-GSM devices  
141 that include accelerometers from e-obs digital telemetry. The setting of the GPS/ACC  
142 devices varied depending on weather conditions and the power level of the batteries (see  
143 Table S1). Except for those birds that died or whose device failed (N=15), we tracked all  
144 the vultures between their capture day and December 2017.

145

#### 146 ***Identification of feeding events and diet description***

147 For each tracked vulture, we identified potential feeding events using *Accelerater*, a  
148 supervised learning algorithm (<http://accapp.move-ecol-minerva.huji.ac.il/>; [39])  
149 implemented with validated samples recorded in feeding stations [16,18]. We recorded  
150 11,636 possible feeding events; from these, we visited 4,372 locations during fieldwork  
151 campaigns, confirming feeding by vultures in 3,338 events (efficiency to locate feeding  
152 events: 76.35%). For each event, we recorded: i) individual identifier of the vulture/s  
153 involved; ii) coordinates of the feeding events, grouping them in UTM 10 x10 km cells;  
154 iii) the feeding site, classified into seven categories: *random* (i.e. carcasses not associated  
155 with infrastructures), *hunting property*, *extensive farm*, *intensive farm*, *carcass dumping*  
156 *site*, *landfill*, and *other* (see Figure 1 for details); iv) the origin of the carcass, according to  
157 five groups: *livestock*, *wild*, *mixed* (i.e., carcasses from both livestock and wild ungulates  
158 found together), *rubbish*, and *indeterminate* (e.g., dogs, rests of human food or whose  
159 origin could not be established); and, where the identification was possible, v) the species

160 to which the carcass/es belonged. If there was more than one carcass, the most abundant  
161 species was recorded.

162 In addition, when access to the feeding sites was prevented (e.g., steep terrain or  
163 private property), we identified feeding sites of GPS-tracked vultures by crossing expert  
164 opinion and official data on livestock and hunting areas from the Spanish Ministry of  
165 Agriculture, Fisheries and Food [40,41]. Thanks to this information, we identified 1,493  
166 additional feeding events. Thus, our final dataset was composed of 4,831 feeding events  
167 (Figure 1), representing 41.52% of the total feeding events identified by GPS-tracking data.  
168 This dataset excludes individuals with less than 30 feeding events recorded, being the total  
169 number of individuals studied 55, 29 from the Northern population (15 females and 14  
170 males) and 26 from the Southern population (11 females and 15 males).

171 Then, we compared the proportion of feeding events at different feeding sites and  
172 with different carrion origin between populations and sexes, using chi-square tests [42].  
173 We did not analyze seasonal and interannual patterns because feeding events were not  
174 evenly distributed among seasons and years.

175

### 176 *Intrapopulation dietary dissimilarity*

177 We measured vultures' dietary dissimilarity (separately for feeding site and carcass origin)  
178 using the E-index [43]. This index calculates the pairwise overlap in diet for all the studied  
179 individuals and averages it for each population (in our case, Northern and Southern). E  
180 ranges from 0 (identical diets) to 1 (completely different diets). We randomly selected 30  
181 observations for each individual and recalculated the metrics 100 times using different  
182 subsets of feeding events. Then, we compared the E-values (i.e., the distribution of 100



183 values for each population obtained using subsets of 30 observations for each individual)  
184 between the two populations using an ANOVA. Model residuals were normally distributed,  
185 and variance was homogenous. We repeated this procedure to explore potential differences  
186 in diet related to sex. We were not able to test the interaction of both factors (population  
187 and sex) together because of the nature of the dataset, that only allows calculating the E-  
188 index separating the data into two groups. However, a visual inspection of the data does  
189 not lead us to suspect the existence of such interaction (see Figure 2).

190

### 191 *Dietary differences in relation to the shared and non-shared foraging areas*

192 We compared the diet (separately for feeding site and carcass origin) of individuals within  
193 the shared foraging area (See Figure S2 for details of shared area delimitation) using  
194 PERMANOVAs, according to their population of origin and sex, considering only those  
195 individuals that used this area (N=18 individuals, 14 from the Southern and 4 from the  
196 Northern populations). Given the low number of feeding events within the shared foraging  
197 area, we used a random subset of 10 observations for each individual and calculated the  
198 PERMANOVAs 1000 times.

199

### 200 *Vulture co-occurrence and network patterns*

201 We used the co-occur package in R [44] to calculate if individuals co-occurred more often  
202 than expected by random. We considered that two individuals co-occurred when both had  
203 at least one feeding event in the same UTM 10x10 km cell. We run the analyses for i) all  
204 individuals together, ii) separating between populations and iii) sexes, and iv) observations  
205 in the shared foraging area.

206           Additionally, we evaluated the topology of the network of spatial interactions  
207 among individuals, separately for 1) all the foraging observations and 2) observations in  
208 the shared foraging area. For each of these two datasets, we calculated two metrics  
209 describing the structure at the network level and four at the node (i.e., individual) level. At  
210 the network level, we calculated i) modularity and ii) cluster metrics. Both metrics indicate  
211 if the network is formed by nodes that interact more among them than with nodes from  
212 other modules. However, while the modularity index was calculated for the incidence  
213 matrix (i.e., a  $n \times m$  matrix where rows  $n$  are UTM 10x10 km cells and columns  $m$  are  
214 individuals, and each cell indicates the number of times an individual was found in a cell),  
215 the cluster coefficient was calculated for the adjacency matrix (a  $m \times m$  matrix where each  
216 cell indicates the number of times that two individuals co-occurred). For modularity, we  
217 used the Q metric with the *bipartite* package [45] in R; for clusters, we calculated the  
218 clustering coefficient with the *igraph* package [46] in R. To identify if the modularity and  
219 the cluster coefficients were larger than expected by random, we created 100 random  
220 matrices where the proportion of interactions per column and row are kept constant, and  
221 we compared the modularity and clustering observed with the ones found for those random  
222 matrices. At the node level, we used *bipartite* [47] to calculate: i) normalized degree, i.e.,  
223 the proportion of realized interactions of the node; ii) weighted closeness, i.e., the average  
224 weighted distance that separate nodes in a network; iii) within-module connectivity ( $z$ );  
225 and iv) between-module connectivity ( $c$ ). Within- and between-module connectivity are  
226 descriptors on how good a node is as a connector inside its module or among different  
227 modules, respectively. We finally compared the node-level metrics between the two  
228 datasets (including all observations and observations only in the shared foraging area)

229 using Mann-Whitney U tests.

230

## 231 **Results**

### 232 *Vultures' diet*

233 Regarding feeding site, most feeding events occurred in intensive farms (31.0% feeding  
234 events) and carcass-dumping sites (29.3%). In relation to carcass origin, 47.3% and 24.9%  
235 of the events corresponded to livestock and wild ungulates, respectively. We were able to  
236 identify the species to which the carcass belonged in 82.7% of the feeding events. The most  
237 frequently recorded species were sheep/goat (*Ovis aries/Capra aegagrus hircus*; 46.0% of  
238 feeding events were the species was identified), followed by pig (*Sus scrofa domestica*;  
239 13.2%). Moreover, 34.5% of the feeding events where the species was identified included  
240 places with more than one prey species, mostly sheep, goats and pigs (Figure S3).

241 Both vulture populations differed in their preferences of feeding sites ( $\chi^2=1295.5$ ,  
242  $df=6$ ,  $p<0.01$ ) and carrion origin ( $\chi^2=1860.9$ ,  $df=4$ ,  $p<0.01$ ; Figures 2 and S4 and S5).  
243 Vultures from the Northern population, which was characterized by a larger and more  
244 predictable ungulate carrion offer than the Southern population, most frequently visited  
245 carcass dumping sites and intensive farms (36.3% and 34.6%, respectively), followed by  
246 landfills (10.7%). Accordingly, the main resources consumed there were livestock (85%)  
247 and rubbish (11.5%). In contrast, vultures from the Southern population visited a greater  
248 variety of feeding sites, mainly hunting properties and intensive farms (26.6% and 24.0%,  
249 respectively). Consequently, diet there was mainly composed of livestock, followed by  
250 wild ungulates (68.3% and 31.6%, respectively).

251 We also observed differences in the feeding sites visited by male and female

252 vultures ( $\chi^2=79.92$ ,  $df=6$ ,  $p<0.01$ ), as well as in the origin of the carcasses consumed by  
253 each sex ( $\chi^2=93.03$ ,  $df=4$ ,  $p<0.01$ ; Figures 2 and S4). Differences between sexes were  
254 stronger in the Southern population, with females using hunting properties more frequently  
255 than males (35.7 vs. 18.4%, respectively) and visiting intensive farms and carcass dumping  
256 sites less frequently than males (21.0 vs. 26.7% for intensive farms, respectively; 13.0 vs.  
257 18.6% for dumping sites, respectively).

258

### 259 *Intrapopulation dietary dissimilarity*

260 The diet of the individuals within the same population was in general not very different, as  
261 shown by the intermediate to low values of dietary dissimilarity (measured with E-index  
262 (average E-index: 0.226, range: 0.196-0.264). However, E-index was consistently larger  
263 among individuals from the Southern population, both for feeding site (average E-index  
264 for vultures from Southern and Northern populations: 0.225 and 0.214, respectively;  
265 ANOVA  $F_{1,198}=5146$ ,  $p<0.001$ ) and carcass origin (E-index: 0.323 and 0.160, respectively;  
266 ANOVA  $F_{1,198}=17.4$ ,  $p<0.001$ ; Figures 2, S4 and S5). Males presented higher values of  
267 diet dissimilarity than females for feeding site (E-index for males and females: 0.334 and  
268 0.297, respectively; ANOVA  $F_{1,198}=301.1$ ,  $p<0.001$ ), but not for carcass origin (E-index:  
269 0.334 and 0.339, respectively; ANOVA  $F_{1,198}=1.97$ ,  $p=0.162$ ).

270

### 271 *Dietary differences in the shared and non-shared foraging areas*

272 The diet of vultures within the shared foraging area differed significantly according to their  
273 population of provenance (for feeding site,  $F_{1,16}$ , mean value of 1000 PERMANOVAS  
274 using a different subset of 10 dietary observations: 5.600, range: 2.670-10.438; for carcass

275 origin,  $F_{1,16}$ , mean: 5.650, range: 2.639-10.973; all  $p < 0.05$ ; see Figure S5), suggesting that  
276 individual vulture diets are mostly driven by learnt cultural traits. Most comparisons were  
277 not significant between sexes (for feeding site,  $F_{1,16}$ , mean: 4.209, range: 0.909-11.537,  
278 75% of the  $p$ -values were higher than 0.05; for carcass origin,  $F_{1,16}$ , mean: 4.110, range:  
279 1.291-9.630, 84.3% of the  $p$ -values were higher than 0.05).

280

### 281 *Co-occurrence and network patterns*

282 All positive spatial co-occurrences were found among individuals from the same  
283 population, while almost all negative co-occurrences involved individuals from different  
284 populations (Figure S6), indicating that individuals from the same population tended to co-  
285 occur together more often than expected by chance. The percentages of positive, negative  
286 and random co-occurrences were 72.8, 0.8 and 26.4, respectively, for the Northern  
287 population, and 40.1, 0.3 and 59.6, respectively, for the Southern population. The same  
288 pattern was found when individuals were separated by sex, as well as when including only  
289 data from the shared foraging area (Figure S6). However, it is important to notice that when  
290 we analyzed the co-occurrences within the shared area, all positive co-occurrences were  
291 detected between individuals from the Southern population. This is because for the  
292 Northern population there was only sufficient information to run the analyses for two  
293 individuals, which showed a random co-occurrence pattern.

294         These results were consistent with the network approach (all  $p < 0.05$ ). In relation to  
295 the network level, we found that both datasets were significantly modular and clustered  
296 (Table S2 and Figure 3). Almost all modules were formed by individuals from the same  
297 population. There was only one module formed by two individuals from different

298 populations. The clusters never grouped included individuals from different populations.  
299 The same pattern was found for all the individuals and for those from the shared foraging  
300 area. Also, figure 3 also clearly shows how individuals from the Northern population share  
301 more links (and thus, co-occur more) than those of the Southern population. At the node  
302 (i.e., individual) level, we found that the individuals at the shared foraging area had a  
303 significantly larger normalized degree (i.e., co-occurred more with other individuals) and  
304 closeness (i.e., individuals where more densely connected; Table 1) than in the whole area,  
305 as can be seen in Figure 3. Regarding the connectivity-related metrics, within-module  
306 connectivity was higher in the whole area. The average among-modules connectivity was  
307 the same for the two networks, but the minimum and maximum values were smaller for  
308 the nodes at the shared foraging area (Table 1). These node-level values are in agreement  
309 with the more modular pattern of the network representing the whole area. Overall, these  
310 results suggest that the individuals tend to appear closer to other individuals of their  
311 population and that this pattern is weaker but still maintained for individuals sharing their  
312 foraging area.

313

## 314 **Discussion**

315 Our study highlights that even super-specialist feeders such as obligate scavengers may  
316 present considerable individual variation in their foraging strategies and resources  
317 consumed. In particular, our results show that griffon vultures exhibit a previously  
318 unknown level of individual dietary specialization, driven by resource availability and sex,  
319 and heavily modulated by vulture culture (i.e., social learning). This finding calls for the

320 need of including cultural traits in Optimal Foraging models, especially in those species  
321 that strongly rely on social information while foraging, such as vultures [10].

322         We found that vultures of the Northern population frequently used anthropic and  
323 predictable resources, such as those that are present in landfills, while vultures of the  
324 Southern population fed on more unpredictable resources, such as wild ungulates' carrion.  
325 Also, Northern vultures tended to co-occur more and are more interconnected than  
326 Southern vultures. These patterns may be primarily explained by the higher availability of  
327 predictable carrion sources in the Northern population compared to the Southern  
328 population [36] and support previous studies suggesting that anthropic resource  
329 homogenization can promote dietary specialization [48].

330         Within this overall context, we also found that sex may introduce a further source  
331 of individual diet variation, with males being more likely to consume predictable resources  
332 than females. Sexual partitioning of the foraging niche is a relatively common  
333 phenomenon. It is usually based on reproductive determinants, such as breeding status and  
334 parental investment, as observed in some seabirds [49,50]. In addition, it can be driven by  
335 the dominance of one sex over the other through social hierarchy [51] or even direct  
336 physical competition [52]. In the case of the griffon vulture, a gregarious species without  
337 marked sexual dimorphism, sexual segregation of diet could be due to social factors, as  
338 suggested for a related species (the Egyptian vulture [51]). However, identifying the  
339 mechanisms behind sex-related differences in griffon vulture diet requires further  
340 investigation on the reproductive investment and social structure of the studied  
341 populations. Independently of the cause, the higher reliance of males on the most  
342 predictable resources could be an ecological trap, as individuals are attracted to seemingly

343 beneficial but risky habitats or resources [53]. In our study system, the consumption of  
344 predictable resources, such as carrion in landfills or intensive livestock farms, entails  
345 greater human-related risks, including greater exposure to poison, pharmaceuticals, and  
346 electrocution and collision in power lines [18,30], which, in turn, might cause the higher  
347 mortality rates and lower health status described for male vultures in the Northern  
348 compared to the Southern study populations [30,54].

349 Consistent with the “cultural trait” scenario, we found that inter-population  
350 differences in foraging and diet remained even in the shared foraging area, where vultures  
351 preferentially co-occurred and were more connected to individuals from their own  
352 population. This indicates that individual vultures maintain the foraging preferences of  
353 their populations even far from them, feeding on the resources they use to consume in their  
354 areas of origin. Thus, foraging and diet specialization in vultures seem to strongly depend  
355 on cultural conformity, according to the predominant resources in their area of origin, thus  
356 supporting the “cultural trait” hypothesis. Cultural conformity occurs when individuals  
357 imitate the cultural information transferred by conspecifics, which have been shown to  
358 influence mating and foraging decisions in mammals and other birds [15,55]. Thus, social  
359 learning might shape the foraging niche of individuals [56]. We posit that the high  
360 cognitive capacity of vultures [57] could facilitate complex social behaviors and the  
361 transmission and assimilation of cultural traits.

362 The coexistence of both cultural lineages in the shared foraging area could be  
363 facilitated by resource heterogeneity. In this area, we found a diverse variety of abundant  
364 carrion resources, which may attract vultures from very distant populations with different  
365 foraging strategies resulting from distinct cultural backgrounds. Thus, the identified shared



366 foraging area, which is characterized by (savannah-like landscapes called “dehesas”), may  
367 act as a key area for the conservation of the griffon vultures in the Iberian Peninsula and,  
368 consequently, in Europe [28]. Further studies could explore if the use of this area by  
369 foraging vultures may be subject to seasonal or inter-annual changes, which could be  
370 especially relevant for those individuals whose diet is based on resources with a clear  
371 seasonality, such as game remains.

372 To conclude, we showed that carrion is a much more heterogeneous resource than  
373 previously thought, as reflected by the strong individual dietary differences observed in the  
374 griffon vulture, an obligate scavenger. Future research may focus on how individual dietary  
375 variations affect vultures’ fitness and scale up to population dynamics, as well as on the  
376 mechanisms and spatio-temporal dimension of vulture culture. The increasing  
377 homogenization of carrion resource towards anthropic and predictable sources [36] could  
378 led to important changes in cultural traits and disruptions of feeding-related evolutionary  
379 processes [10]. Our findings call for strict protection of those areas that allow the  
380 development of cultural lineages based on wild ungulates and extensive livestock, which  
381 moreover represent safer food sources for vultures.

382

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398

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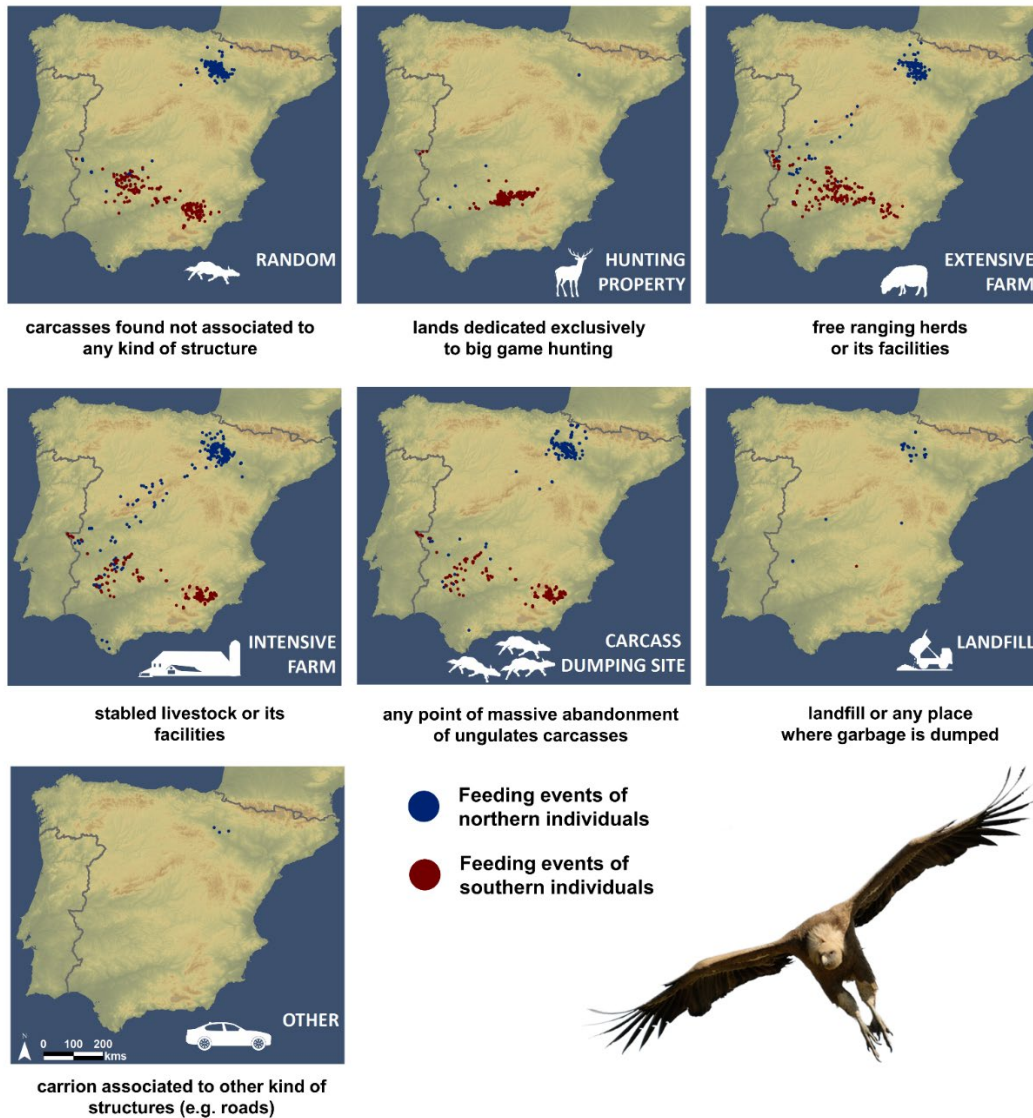
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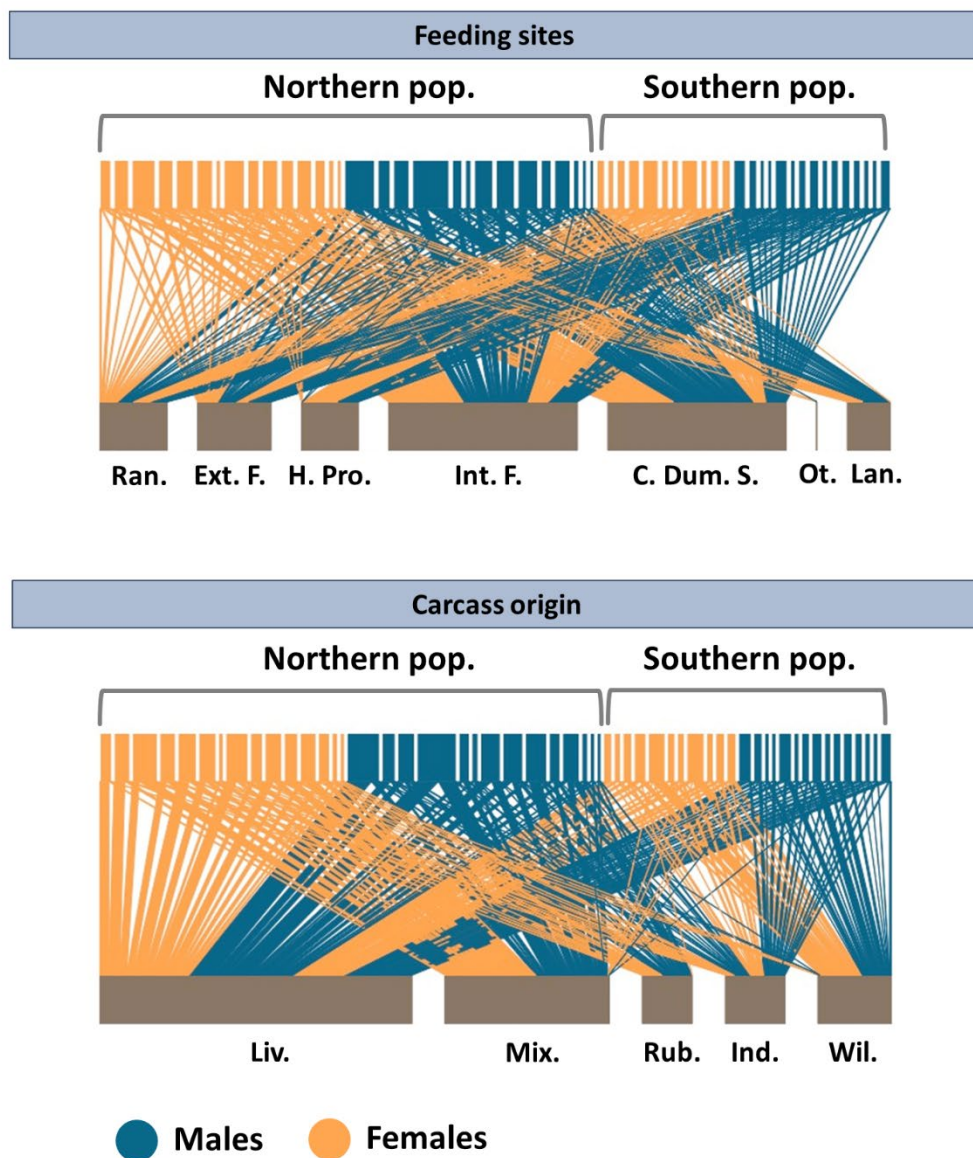
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537 **Figures and Tables**  
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 541 **Figure 1:**  
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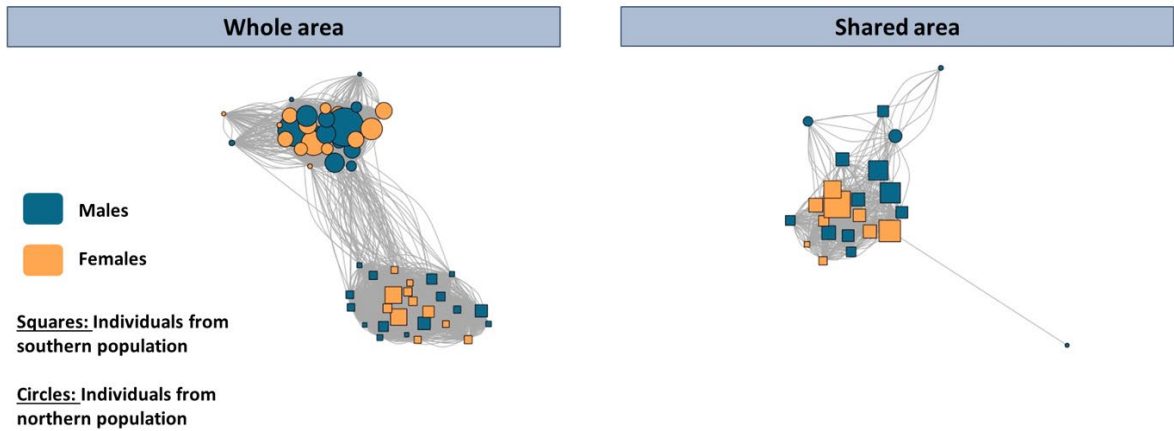
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545 **Figure 2:** Representation of the diet of each GPS-tracked individual as a function of the  
 546 feeding sites visited (upper panel) and the origin of the carrion consumed (lower panel).  
 547 Each vertical column of the upper row of the panels represents an individual, and its  
 548 width is proportional to the number of events available for each one. Abbreviations in the  
 549 upper panel: Ran: random, carcasses, i.e., those that were not found associated with any  
 550 kind of structure; Ext.: extensive farms, free ranging herds or its facilities; Hun.: hunting  
 551 properties, i.e., lands dedicated exclusively to big game hunting; Int.: intensive farms,  
 552 stabled livestock or its facilities; Dum.: carcass dumping sites, i.e., any point of massive  
 553 abandonment of ungulate carcasses; Lan.: landfills or any other place where garbage is  
 554 dumped; Oth.: other types of carrion, such as carcasses associated with other kinds of  
 555 structures (e.g., roads). Abbreviations in the lower panel: Liv: livestock or domestic

556 ungulate carcasses; Wil.: wild ungulate carcasses; Mix: mixed carcasses, i.e., carcasses  
557 from both domestic and wild ungulates; Rub: rubbish, human waste; Ind.: indeterminate,  
558 i.e., carcasses whose origin was uncertain.





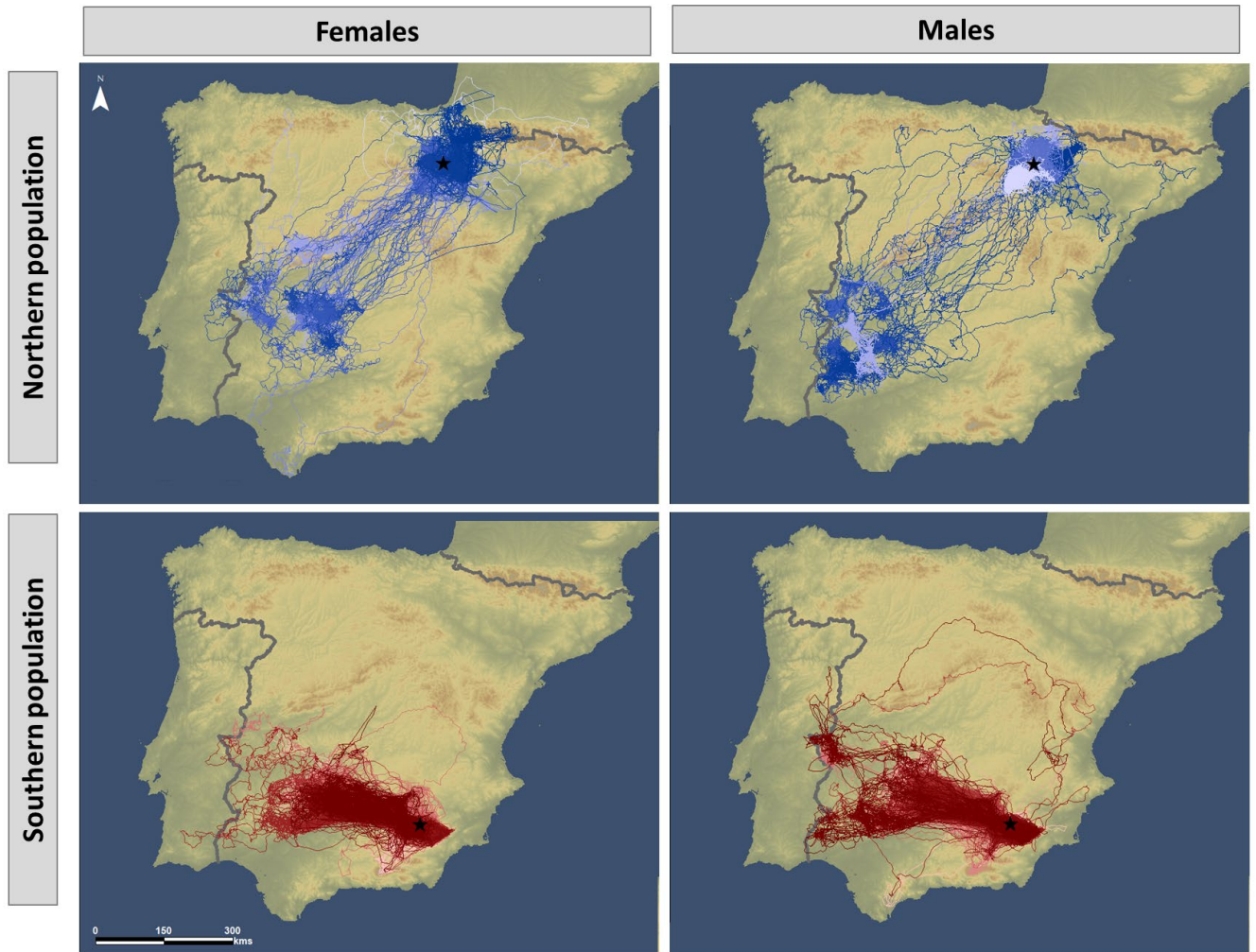
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561 **Figure 3:** Networks showing co-occurrence patterns among individuals in the whole  
 562 study area and in the shared foraging area. Each node (square or circle) represents one  
 563 individual, and a link indicates that both individuals co-occurred in the same UTM 10x10  
 564 km cell. Circles: individuals from the Northern population; squares: individuals from the  
 565 Southern population.

566 **Table 1.** Summary of the node-level network values for individuals, separately for the  
 567 whole study area and shared foraging area. We show the mean, standard deviation,  
 568 minimum and maximum values found in each dataset for normalized degree, weighted  
 569 closeness, among-modules connectivity (c) and within-modules connectivity (z). We also  
 570 show the Mann-Whitney U and the p-value comparing the node values among the  
 571 individuals in the whole area vs. the shared foraging area.  
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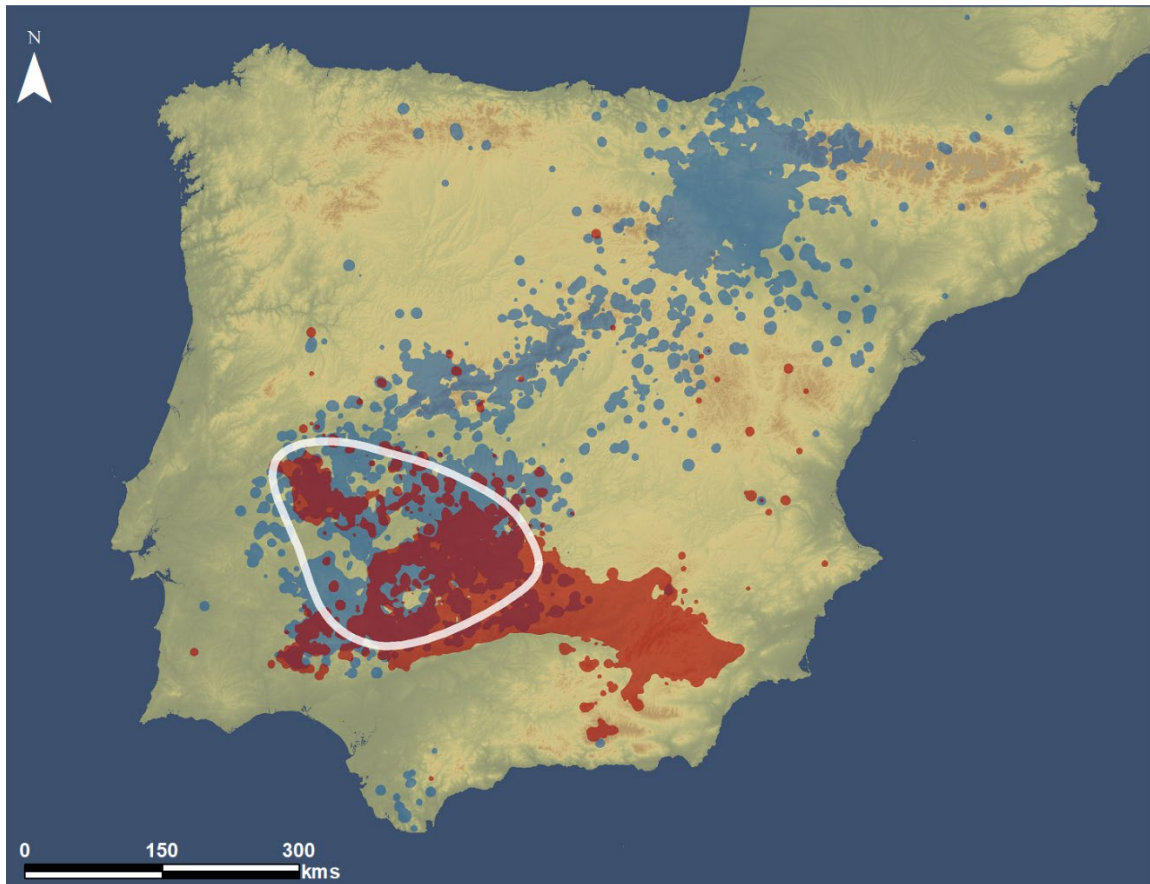
Metric	whole area				shared area				u	p
	mean	sd	min	max	mean	sd	min	max		
Degree	0.065	0.022	0.013	0.142	0.099	0.041	0.032	0.204	4290.0	<0.001
Closeness	0.005	0.002	0.002	0.007	0.030	0.008	0.009	0.040	4290.0	<0.001
c	0.288	0.154	0	0.595	0.390	0.152	0.150	0.661	4262.5	<0.001
z	0.000	0.953	-1.450	2.259	0.000	0.804	-1.627	1.578	2210.0	0.015

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577 **Figure S1.** Movement patterns of the individuals tracked by GPS during the study period,  
578 separated by sex and population. Each tone within the colour scale (blue for the Northern  
579 population and red for the Southern population) represents an individual. Black stars  
580 indicate capture locations.  
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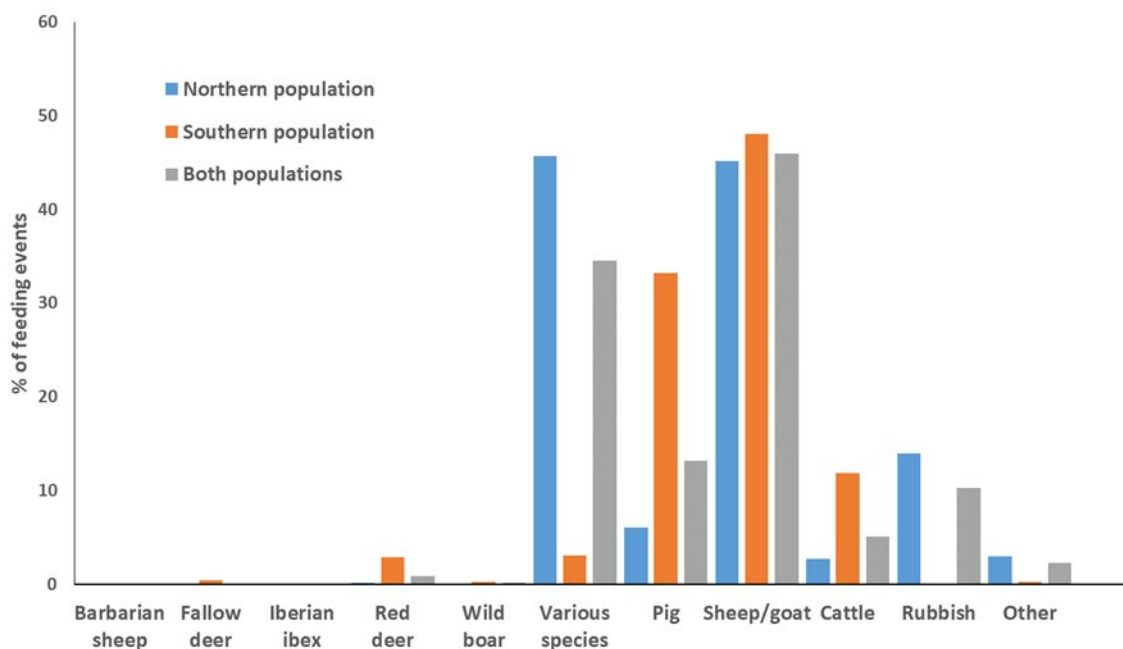
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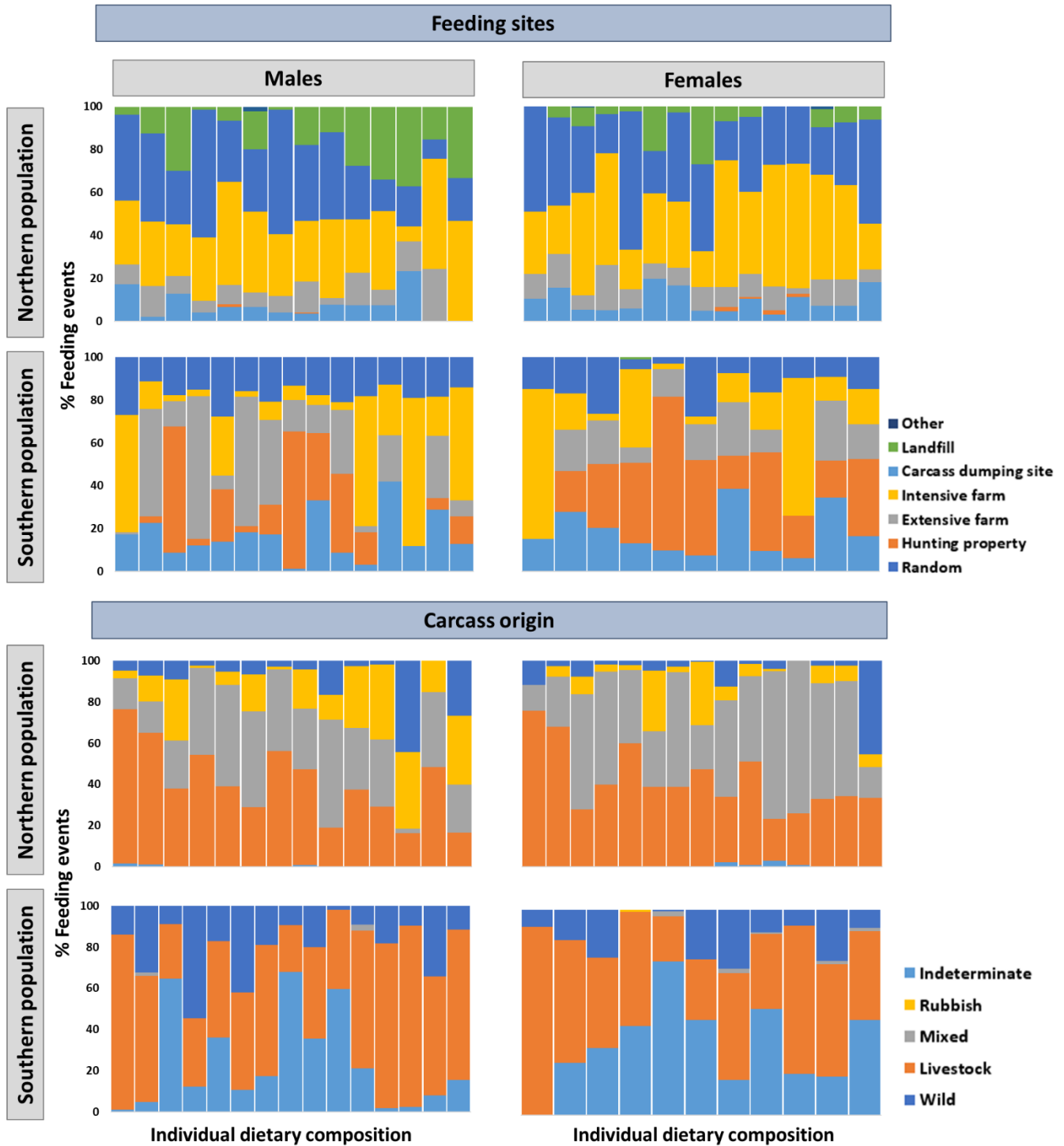
585 **Figure S2.** Blue and red areas represent the total foraging area of Northern and Southern  
586 population respectively. These areas were calculated as 95% Kernel Density Estimation  
587 of the whole the overall locations of all the individuals in each population. White line  
588 delimits foraging area shared by the two studied vulture populations. To obtain it, we  
589 divided the Iberian Peninsula in UTM 10x10 km grids and categorized the cells  
590 depending on whether they contained GPS locations of vultures or not. Then, we defined  
591 the shared foraging area as the contour of the 95% of the cells containing GPS locations  
592 from both populations.



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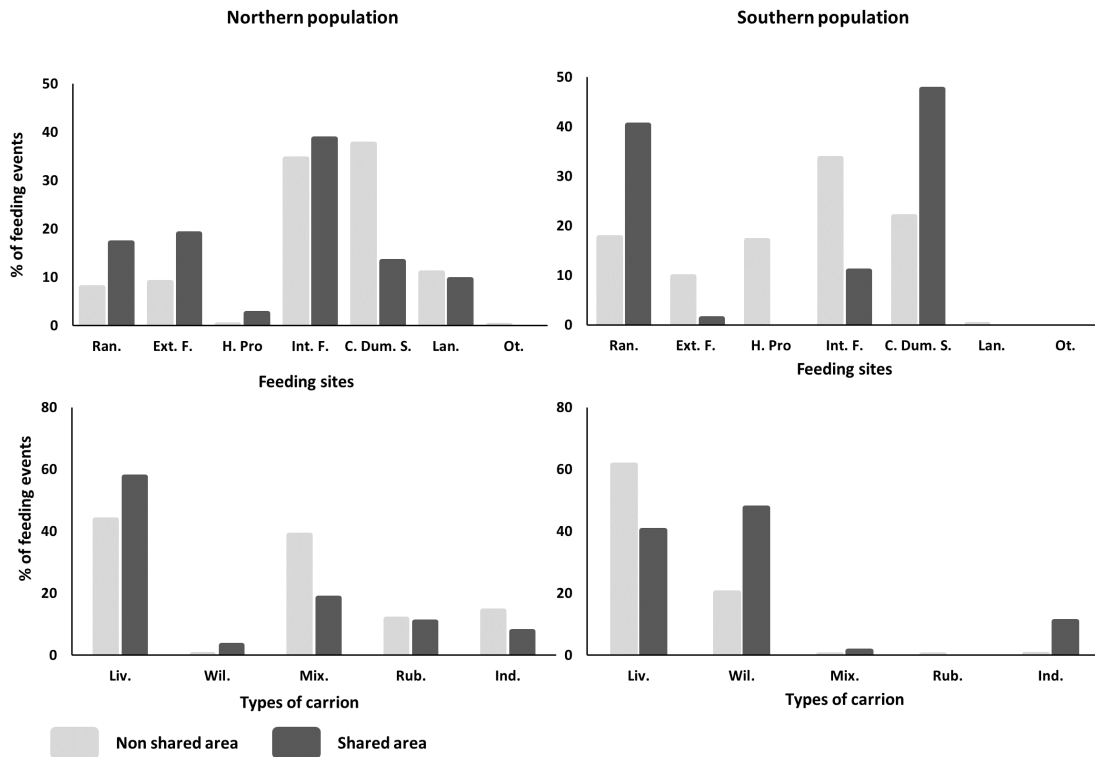
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595 **Figure S3.** Prey species found in the field survey of the feeding events of the GPS-  
 596 tracked vultures, according to population. The figure shows the proportion of feeding  
 597 events that belonged to each category. Only feeding events where the prey species was  
 598 identified are represented.

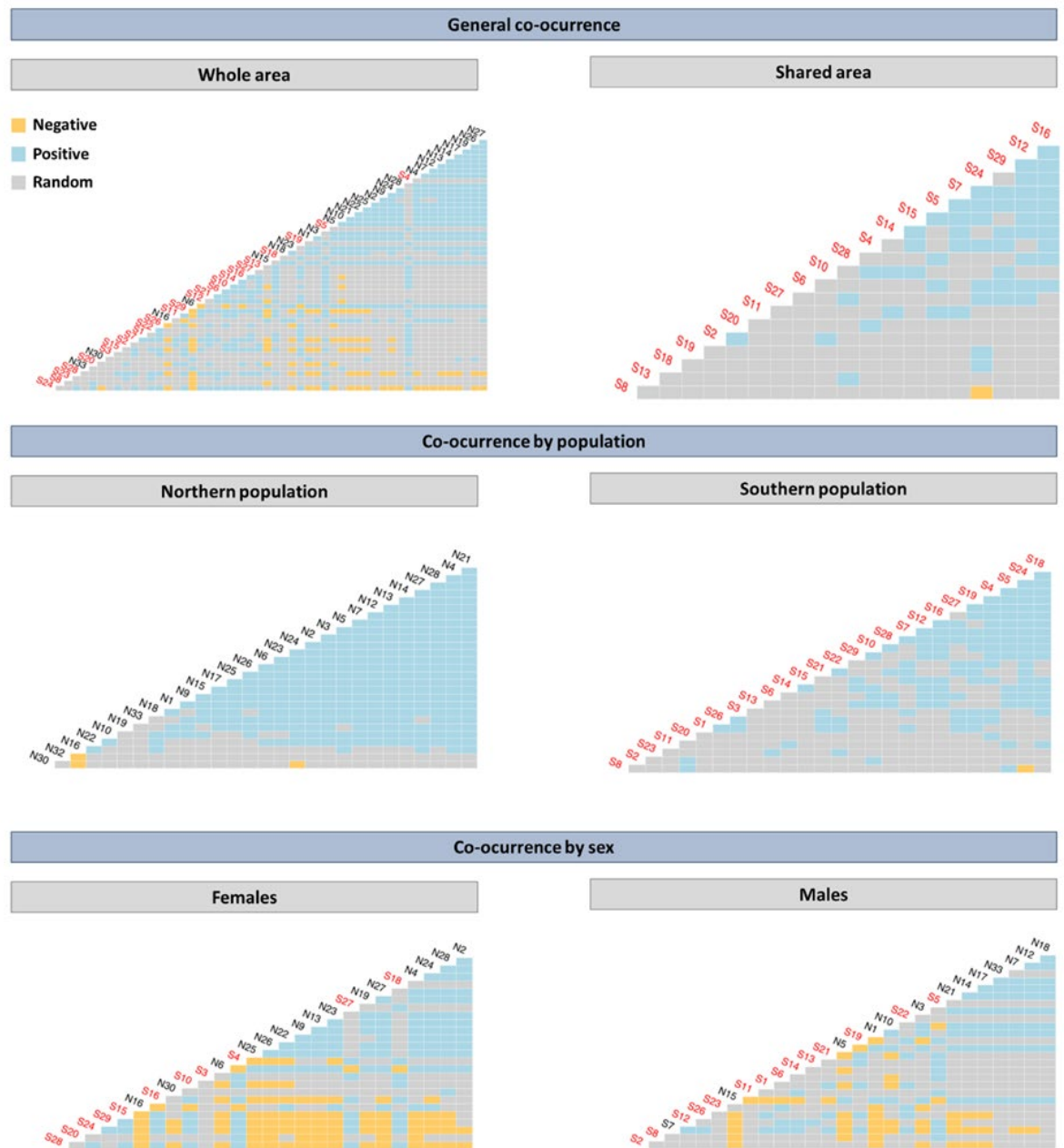


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**Figure S4.** Diet partitioning of the GPS-tracked griffon vultures according to carcass feeding site (upper panel) and origin (lower panel), separately for each population and sex. Upper row of each panel represents Northern population and lower row represents Southern population. Each column represents one vulture individual. See Figure 2 for a detailed description of feeding sites.



607  
 608 **Figure S5.** Population differences in the percentage of feeding events inside and outside  
 609 the shared area according to the feeding site visited and the type of carrion consumed.  
 610 Abbreviations in the upper panel: Ran: Random, carcasses found not associated to any  
 611 kind of structure; Ext. F.: Extensive farms, free ranging herds or its facilities; H. Pro.:  
 612 Hunting properties, lands dedicated exclusively to big game hunting; Int. F.: Intensive  
 613 farms, stabled livestock or its facilities; C. Dum. D.: Carcass dumping sites, any point of  
 614 massive abandonment of ungulates carcasses; Lan.: Landfills, landfill or any place where  
 615 garbage is dumped; Ot.: Other, carrion associated to other kind of structures (e.g., roads)  
 616 Abbreviations in the lower panel: Liv: Livestock, domestic ungulates carcasses Wil.:  
 617 Wild ungulate carcasses; Mix: Mixed, carcasses from both, domestic and wild ungulates;  
 618 Rub: Rubbish, human waste; Ind.: Indeterminate: carcasses it was impossible to establish  
 619 their origin



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623 **Figure S6.** Co-occurrence patterns for the studied individuals divided by focus area  
 624 (upper panel), population (central panel) and sex (bottom panel).). Each line represents  
 625 one individual. Each cell represents the co-occurrence pattern (positive, negative or  
 626 random) of each pair of individuals. First letter of the individual code represents the  
 627 population of origin of each individual (N= Northern; black letters; S= Southern; red  
 628 letters). Only individuals with non-random co-occurrences are shown. Individuals are



629 ordered starting from those with the most negative interactions to those with the most  
630 positive interactions.

631 **Table S1.** GPS/ACC device settings and time elapsed between consecutive locations.  
 632 Devices were activated one hour before sunrise and turned off one hour after sunset.  
 633 High-performance settings were active continuously except if we detected a low battery  
 634 status for several days. We then activated the low-performance setting until the battery  
 635 recovered normal status. During the study period, the time between consecutive locations  
 636 ranged from 5 seconds to 14.9 h with a median of 5 min. ACC samples had a length of  
 637 10-second per burst with a frequency of 8.33 Hzs. In cases of low battery level, the  
 638 setting of ACC the setting varied according to weather forecasts.

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		Battery status			
		Full	Non-full	Close to security level	Under security level
GPS	Low-performance setting	10 min	30 min	1 h	1 day
	High-performance setting	5 min	20 min	30 min	1 day
ACC		2.5 min	2.5 min	Variable	Variable

643

644 **Table S2.** Results of the network-level analyses. For each dataset (whole study area and  
 645 shared foraging area), we show the modularity and clustering coefficients, the mean  
 646 coefficients for the random (null) matrices, their standard deviations, the z-score  
 647 [(observed value – mean value of the null networks) / SD of the null networks] and the p-  
 648 value.  
 649

Metric	Dataset	Value	Mean null	SD null	Z-score	p-value
Modularity	whole	0.513	0.407	0.010	10.260	<0.001
	shared	0.474	0.403	0.010	6.737	<0.001
Cluster	whole	0.228	0.005	0.003	87.974	<0.001
	shared	0.124	0.070	0.023	2.413	0.030

650