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Vulture culture: dietary specialization of an obligate scavenger

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

1. Introduction

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

Causes of dietary specialization include factors related to both the environment (extrinsic) and the individual (intrinsic). First, extrinsic factors, such as prey attributes (e.g. availability, energetic content and predictability), can contribute to define individual dietary differences [2]. Notably, inter- and intraspecific competition may force subordinate or inexperienced individuals to consume

suboptimal or secondary prey [6–8], especially where resources are scarce [9] thus enhancing inter-individual variation. Second, individual preferences can be driven by intrinsic factors associated with phenotypic traits such as body size, sex or social status [4,10,11]. In addition, some individuals are more cautious than others against predator and parasite risks associated with food [12], which may also determine different diets. Social facilitation processes may also result in different individual dietary patterns [13]. For instance, individuals may develop a preference for a particular diet either by imitating their parents during the juvenile stage or by imitating more experienced individuals while foraging in a particular area or on a particular resource. Both extrinsic and intrinsic processes have been shown to be capable of generating cultural patterns with population-level effects in birds and mammals [14,15].

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

According to Optimal Foraging Theory, the net energy gain obtained during feeding is the difference between the energy ingested and the energy used in searching and handling the food [21]. In this scenario, vultures evolved to consume a resource that needs little manipulation but involves high searching cost, which they address via highly efficient foraging strategies [22,23]. Thus, vultures spend much time foraging and rely heavily on social information obtained from conspecifics [24]. Social information transfer leads to two possible foraging scenarios: (a) 'local enhancement', in which vultures feed on carcasses located by other individuals [25], and (b) 'cultural traits', in which vultures learn to detect the most profitable carrion sources or food types from conspecifics [26]. The most straightforward prediction for both hypotheses is that individuals from the same population have similar diets. Given the long-distance movements of *Gyps* vultures [27,28], it is usual for individuals from different populations to converge in an area far from their home colonies [28]. However, whether vultures in these shared areas are locally enhanced by vultures from other populations or retain the cultural traits of their own population is unknown. Thus, exploring the foraging behaviour of vultures from different populations in shared and non-shared foraging areas may help to better understand the determinants of individual vulture foraging decisions.

Here, we combined radiotracking data from GPS and accelerometers and intensive field validation at the large spatial scale to address individual variation in the diet of griffon vultures (*Gyps fulvus*) from two Spanish populations that partially overlap in their foraging areas. We identified not only the diet of every tracked vulture, but also the specific sites where vultures ate, an aspect that has rarely been considered in intrapopulation diet studies at large spatial scale. Our general hypothesis is that obligate scavengers may also exhibit individual dietary specialization, with social learning playing an important role in shaping individual vultures' diet. We expect to find lower variability in the diet of individuals inhabiting areas rich in predictable resources, such as intensive livestock farming, than in undisturbed sites. From previous ecological knowledge on griffon vultures, no clear prediction on how sex may influence individual diets can be delineated. Regarding social information, there are two alternative scenarios: (1) a 'local enhancement' scenario, where individuals from different populations are expected to have similar diets when exploiting shared foraging areas (i.e. areas where these populations forage regularly), and (2) a 'cultural trait' scenario, where individuals from different populations are expected to maintain the dietary preferences of their population of origin and have different diets even in the shared foraging area. Exploring the contribution of cultural traits in vulture diet at the individual level may help to better understand the eco-evolutionary consequences of culture transmission in social species. Furthermore, it might be key to the conservation of vultures, which are globally threatened [29] and particularly vulnerable to anthropogenic hazards while foraging in human-dominated environments [30].

2. Materials and methods

(a) Study species
Griffon vultures are large scavengers weighting 6–11 kg. They are colonial cliff breeders with great flying capacities that allow them to forage over very large areas (up to 32 000 km^2) [28,31]. The diet of this vulture is mainly composed of carcasses of domestic and wild ungulates, with occasional contributions of smaller sized vertebrates [16,32].

(b) GPS-tracking and study areas
We captured 65 adult griffon vultures, 30 individuals in southern Spain ('Southern') between December 2014 and January 2015 and 35 individuals in northern Spain ('Northern') between December 2015 and March 2016. The Southern area is a mountainous region (500–2,107 m.a.s.l.) covered by Mediterranean woodlands and pasturelands, where the main human uses are traditional farming, hunting, forestry and tourism [33]. The Northern area is a flat area (28–659 m.a.s.l.) surrounded by mid-sized mountains (up to 1500 m.a.s.l.) and highly transformed for intensive agriculture, with traditional sheep livestock being replaced by intensive farming [34,35]. As a consequence, carrion sources in the Northern area are more predictable compared to the Southern one [36], although trophic resources can be considered abundant in both areas. In addition to these areas, both vulture populations share a second foraging area in southwestern Spain (electronic supplementary material, figures S1 and S2) where carrion from wild and domestic ungulates is also abundant [36].

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

(c) Identification of feeding events and diet description
For each tracked vulture, we identified potential feeding events using *Accelerater*, a supervised learning algorithm (http://
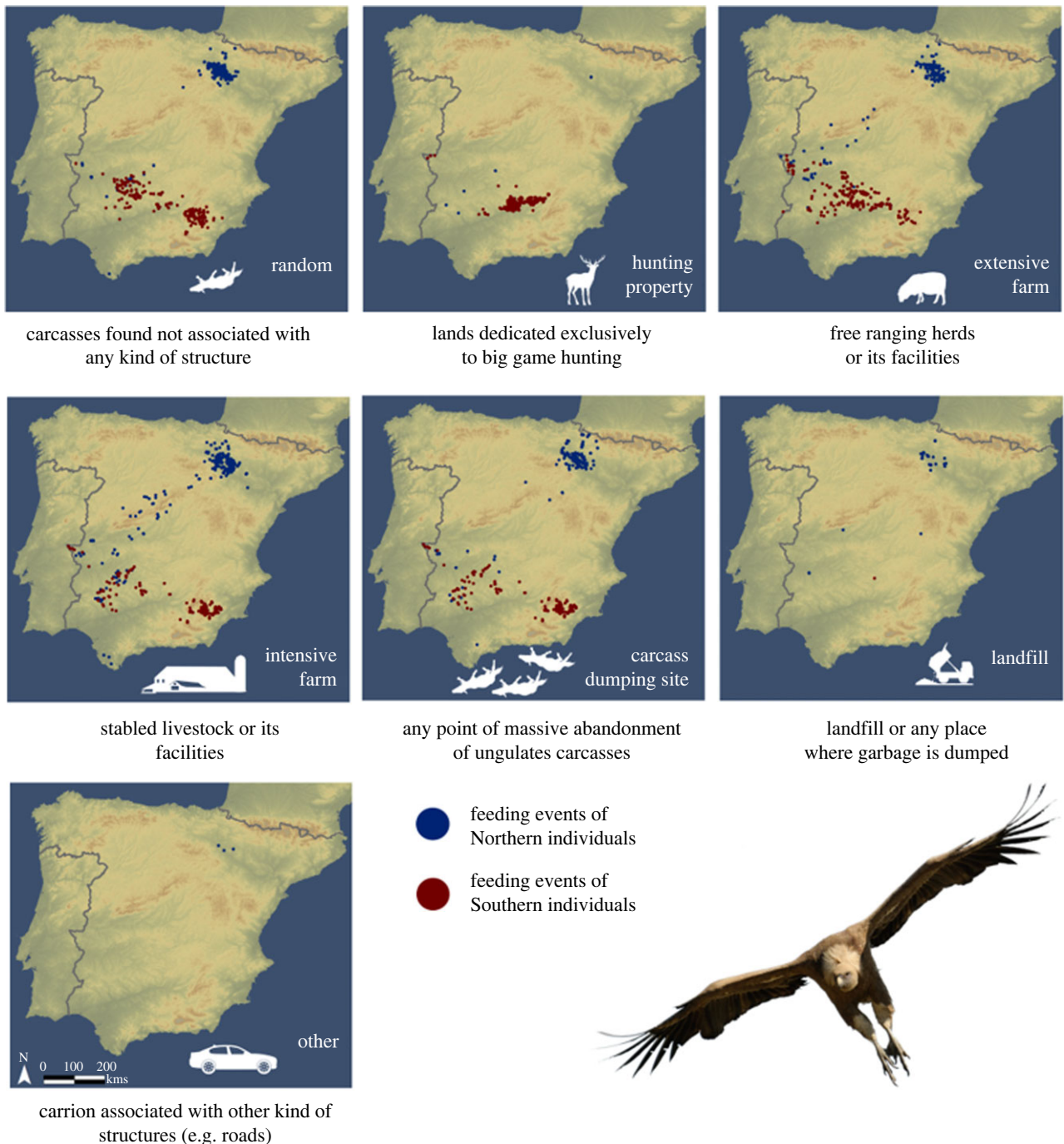
Figure 1. Maps representing the distribution of feeding events by GPS-tracked griffon vultures, according to different feeding sites. Only events used in the statistical analyses are shown. The description of each feeding site is specified under each map.

accapp.move-ecol-minerva.huji.ac.il/; [39]) implemented with validated samples recorded in feeding stations [16,18]. We recorded 11 636 possible feeding events; from these, we visited 4372 locations during fieldwork campaigns, confirming feeding by vultures in 3338 events (efficiency to locate feeding events: 76.35%). For each event, we recorded: (i) individual identifier of the vulture/s involved; (ii) coordinates of the feeding events, grouping them in UTM 10 × 10 km cells; (iii) the feeding site, classified into seven categories: *random* (i.e. carcasses not associated with infrastructures), *hunting property*, *extensive farm*, *intensive farm*, *carcass-dumping site*, *landfill* and *other* (figure 1 for details); (iv) the origin of the carcass, according to five groups: *livestock*, *wild*, *mixed* (i.e. carcasses from both livestock and wild ungulates found together), *rubbish* and *indeterminate* (e.g. dogs, rests of human food or whose origin could not be established); and, where the identification was possible, (v) the species to which the carcass/es belonged. If there was more than one carcass, the most abundant species was recorded.

In addition, when access to the feeding sites was prevented (e.g. steep terrain or private property), we identified feeding sites of GPS-tracked vultures by crossing expert opinion and official data on livestock and hunting areas from the Spanish Ministry of Agriculture, Fisheries and Food [40,41]. Thanks to this information, we identified 1493 additional feeding events. Thus, our final dataset was composed of 4831 feeding events (figure 1), representing 41.52% of the total feeding events identified by GPS-tracking data. This dataset excludes individuals with less than 30 feeding events recorded, bringing the total number of individuals studied to 55, 29 from the Northern population (15 females and 14 males) and 26 from the Southern population (11 females and 15 males).

We compared the proportion of feeding events at different feeding sites and with different carrion origin between populations and sexes using chi-square tests [42]. We did not analyse seasonal and interannual patterns because feeding events were not evenly distributed among seasons and years.
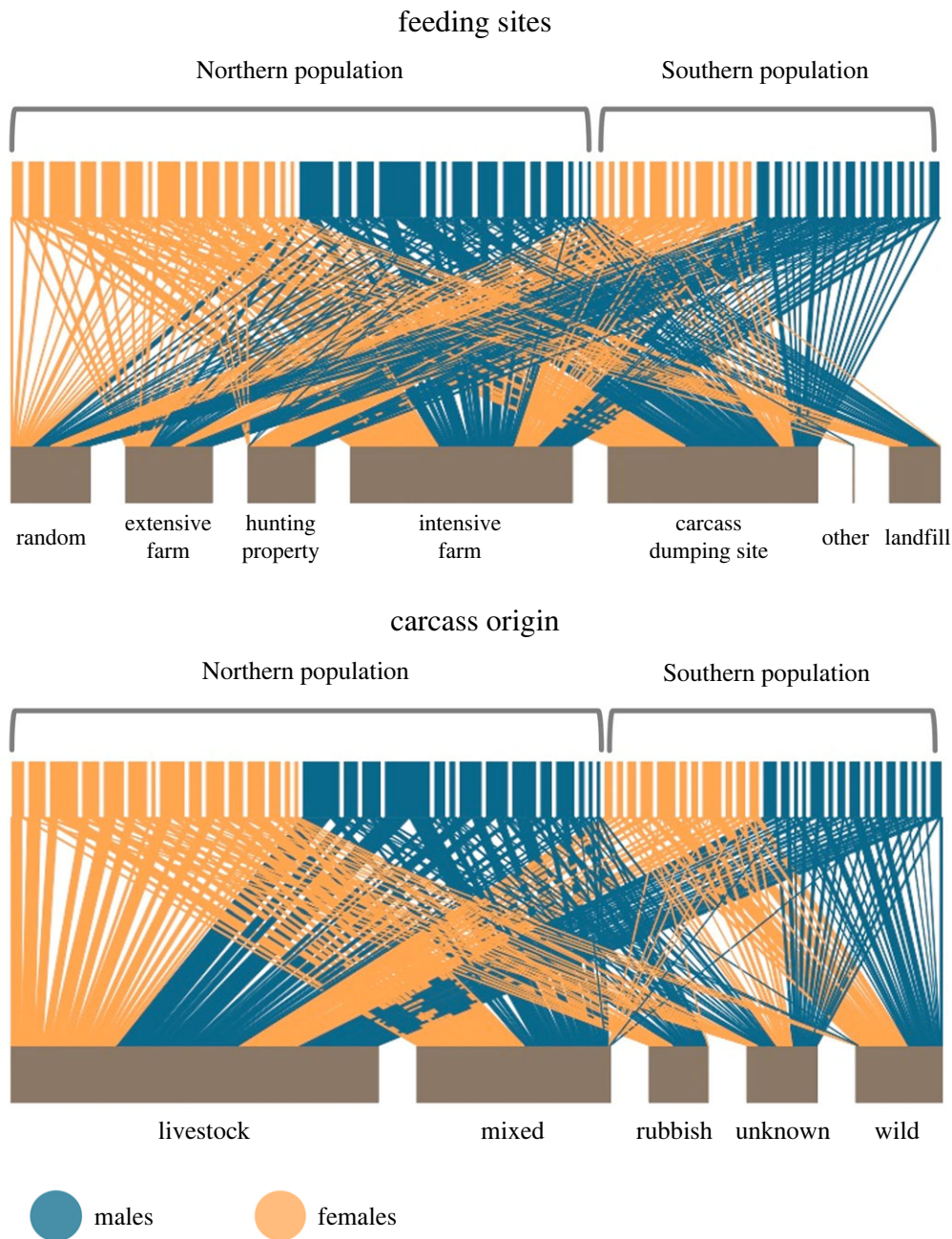
Figure 2. Representation of the diet of each GPS-tracked individual as a function of the feeding sites visited (upper panel) and the origin of the carrion consumed (lower panel). Each vertical column of the upper row of the panels represents an individual, and its width is proportional to the number of events available for each one. Categories in the upper panel: random: carcasses, i.e. those that were not found associated with any kind of structure; extensive farms: free ranging herds or its facilities; hunting properties: lands dedicated exclusively to big game hunting; intensive farms: stabled livestock or its facilities; carcass-dumping sites: any point of massive abandonment of ungulate carcasses; landfills: any other place where garbage is dumped; other: any other type of carrion, such as carcasses associated with other kinds of structures (e.g. roads). Categories in the lower panel: livestock: domestic ungulate carcasses; wild: wild ungulate carcasses; mixed: mixed carcasses, i.e. carcasses from both domestic and wild ungulates; rubbish: human waste; unknown, i.e. carcasses whose origin was uncertain.

(d) Intrapopulation dietary dissimilarity

We measured vultures' dietary dissimilarity (separately for feeding site and carcass origin) using the E-index [43]. This index calculates the pairwise overlap in diet for all the studied individuals and averages it for each population (in our case, Northern and Southern). E ranges from 0 (identical diets) to 1 (completely different diets). We randomly selected 30 observations for each individual and recalculated the metrics 100 times using different subsets of feeding events. We compared the E-values (i.e. the distribution of 100 values for each population obtained using subsets of 30 observations for each individual) between the two populations using an ANOVA. Model residuals were normally distributed, and variance was homogeneous. We repeated this procedure to explore potential differences in diet related to sex. We were not able to test the

interaction of both factors (population and sex) together because E-index only allows to divide the dataset into two groups. However, a visual inspection of the data does not lead us to suspect the existence of such interaction (figure 2).

(e) Dietary differences in relation to the shared and non-shared foraging areas

We compared the diet (separately for feeding site and carcass origin) of individuals within the shared foraging area (see electronic supplementary material, figure S2 for details of shared area delimitation) using PERMANOVAs, according to their population of origin and sex, considering only those individuals that used this area ($n = 18$ individuals, 14 from the Southern and

4 from the Northern populations). Given the low number of feeding events within the shared foraging area, we used a random subset of 10 observations for each individual and calculated the PERMANOVAs 1000 times.

(f) Vulture co-occurrence and network patterns

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

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

3. Results

(a) Vultures' diet

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

Vulture populations differed in their preferences of feeding sites ($\chi^2 = 1295.5$, d.f. = 6, $p < 0.01$) and carrion origin ($\chi^2 = 1860.9$, d.f. = 4, $p < 0.01$; figure 2; electronic supplementary material, figures S4 and S5). Vultures from the Northern population, which was characterized by a larger and more predictable ungulate carrion offer than the Sothern population, most frequently visited carcass-dumping sites and intensive farms (36.3% and 34.6%, respectively), followed by landfills (10.7%). Accordingly, the main resources consumed there were livestock (85%) and rubbish (11.5%). By contrast, vultures from the Southern population visited a greater variety of feeding sites, mainly hunting properties and intensive farms (26.6% and 24.0%, respectively). Consequently, diet there was mainly composed of livestock, followed by wild ungulates (68.3% and 31.6%, respectively).

We also observed differences in the feeding sites visited by male and female vultures ($\chi^2 = 79.92$, d.f. = 6, $p < 0.01$), as well as in the origin of the carcasses consumed by each sex ($\chi^2 = 93.03$, d.f. = 4, $p < 0.01$; figure 2; electronic supplementary material, figure S4). Differences between sexes were stronger in the Southern population, with females using hunting properties more frequently than males (35.7 versus 18.4%, respectively) and visiting intensive farms and carcass-dumping sites less frequently than males (21.0 versus 26.7% for intensive farms, respectively; 13.0 versus 18.6% for dumping sites, respectively).

(b) Intrapopulation dietary dissimilarity

The diet of the individuals within the same population was similar overall, as shown by the intermediate to low values of dietary dissimilarity (measured with E-index (average E-index: 0.226, range: 0.196–0.264). However, E-index was consistently larger among individuals from the Southern population, both for feeding site (average E-index for vultures from Southern and Northern populations: 0.225 and 0.214, respectively; ANOVA $F_{1,198} = 5146$, $p < 0.001$) and carcass origin (E-index: 0.323 and 0.160, respectively; ANOVA $F_{1,198} = 17.4$, $p < 0.001$; figure 2; electronic supplementary material, figures S4 and S5). Males presented higher values of diet dissimilarity than females for feeding site (E-index for males and females: 0.334 and 0.297, respectively; ANOVA $F_{1,198} = 301.1$, $p < 0.001$), but not for carcass origin (E-index: 0.334 and 0.339, respectively; ANOVA $F_{1,198} = 1.97$, $p = 0.162$).

(c) Dietary differences in the shared and non-shared foraging areas

The diet of vultures within the shared foraging area differed significantly according to their population of provenance (for feeding site, $F_{1,16}$, mean value of 1000 PERMANOVAS using a different subset of 10 dietary observations: 5.600, range: 2.670–10.438; for carcass origin, $F_{1,16}$, mean: 5.650, range: 2.639–10.973; all $p < 0.05$; see electronic supplementary material, figure S5), suggesting that individual vulture diets are mostly driven by learnt cultural traits. Most comparisons were not significant between sexes (for feeding site, $F_{1,16}$, mean: 4.209, range: 0.909–11.537, 75% of the p-values were higher than 0.05; for carcass origin, $F_{1,16}$, mean: 4.110, range: 1.291–9.630, 84.3% of the p-values were higher than 0.05).

(d) Co-occurrence and network patterns

All positive spatial co-occurrences were found among individuals from the same population, while almost all negative co-occurrences involved individuals from different
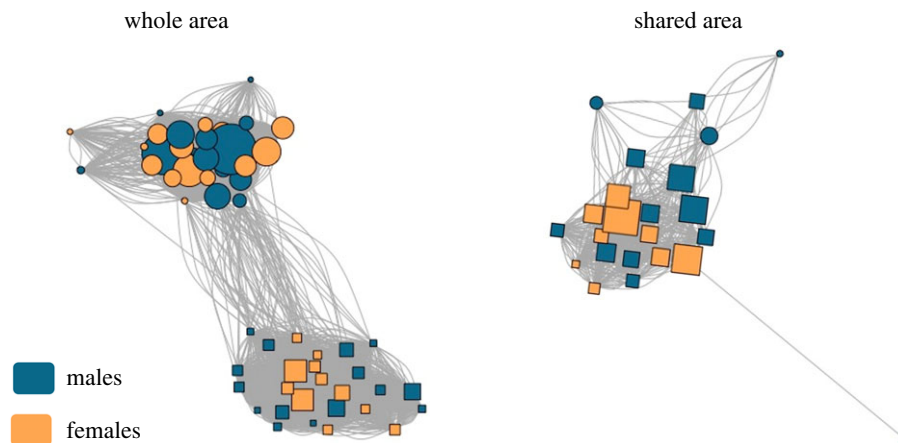
Figure 3. Networks showing clustering patterns among individuals in the whole study area and in the shared foraging area. Each node (square or circle) represents one individual, and a link indicates that both individuals co-occurred in the same UTM 10 × 10 km cell. The size of the circle/square indicates the number of links in that node. Circles: individuals from the Northern population; squares: individuals from the Southern population.

populations (electronic supplementary material, figure S6), indicating that individuals from the same population tended to co-occur together more often than expected by chance. The percentages of positive, negative and random co-occurrences were 72.8, 0.8 and 26.4, respectively, for the Northern population, and 40.1, 0.3 and 59.6, respectively, for the Southern population. The same pattern was found when individuals were separated by sex, as well as when including only data from the shared foraging area (electronic supplementary material, figure S6). However, it is important to notice that when we analysed the co-occurrences within the shared area, all positive co-occurrences were detected between individuals from the Southern population. This is because for the Northern population there was only sufficient information to run the analyses for two individuals, which showed a random co-occurrence pattern.

These results were consistent with the network approach ($p < 0.05$ in all analyses). In relation to the network level, we found that both datasets were significantly modular and clustered (electronic supplementary material, table S2; figure 3). Most modules (total number of modules: 16 for the whole area and 9 for the shared foraging area) were formed by individuals from the same population. Only two modules in the shared foraging area were formed by individuals from different populations. Also, we identified two clusters for the whole area and six for the shared foraging area, with each cluster being formed by individuals from only one of the two populations. As shown in figure 3, individuals from the Northern population shared more links (and thus, co-occurred more) than those of the Southern population. At the node (i.e. individual) level, we found that individuals in the shared foraging area had a significantly larger normalized degree (i.e. co-occurred more with other individuals) and closeness (i.e. individuals where more densely connected) than in the whole area (figure 3; electronic supplementary material, table S3). Regarding the connectivity-related metrics, within-module connectivity was higher in the whole area compared to the shared foraging area. The average among-modules connectivity was the same for the two datasets, but the minimum and maximum values were smaller for the nodes in the shared foraging area (electronic supplementary material, table S3). These node-level values are in agreement with the more modular pattern of the network for the whole area. Overall, these results suggest that the individuals tend to appear closer to other individuals of their population and that this pattern is weaker but still maintained for individuals sharing their foraging area.

4. Discussion

Our study highlights that even specialist feeders such as obligate scavengers may present considerable individual variation in their foraging strategies and resources consumed. In particular, our results show that griffon vultures exhibit a previously unknown level of individual dietary specialization, driven by resource availability and sex, and heavily modulated by vulture culture (i.e. social learning). This finding calls for the need of including cultural traits in Optimal Foraging models, especially in those species that strongly rely on social information while foraging, such as vultures [10].

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

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

Independently of the cause, the higher reliance of males on the most predictable resources could be an ecological trap, as individuals are attracted to seemingly beneficial but risky habitats or resources [53]. In our study system, the consumption of predictable resources, such as carrion in land-fills or intensive livestock farms, entails greater human-related risks, including greater exposure to poison, pharmaceuticals, and electrocution and collision in power lines [18,30], which, in turn, might cause the higher mortality rates and lower health status described for male vultures in the Northern compared to the Southern study populations [30,54].

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

The coexistence of both cultural lineages in the shared foraging area could be facilitated by resource heterogeneity. In this area, we found a diverse variety of abundant carrion resources, which may attract vultures from very distant populations with different foraging strategies resulting from distinct cultural backgrounds. Thus, the identified shared foraging area, which is characterized by (savannah-like landscapes called 'dehesas'), may act as a key area for the conservation of the griffon vultures in the Iberian Peninsula and, consequently, in Europe [28]. Further studies could explore if the use of this area by foraging vultures may be subject to seasonal or interannual changes, which could be especially relevant for those individuals whose diet is based on resources with a clear seasonality, such as game remains.

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

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