

1 **Unravelling the vertebrate scavenger assemblage in the Gobi Desert, Mongolia**

2

3 Adrian Orihuela-Torres^{a*}, Zebensui Morales-Reyes^a, Juan M. Pérez-García^a, Lara

4 Naves-Alegre^a, José A. Sánchez-Zapata^a & Esther Sebastián-González^a

5 ^a Department of Applied Biology, Miguel Hernández University. Avda. Universidad s/n

6 22 03202 Elche, Alicante, Spain; adrian.orihuela89@gmail.com (A.O.T.);

7 zmorales@umh.es (Z.M.R); juanmapg@gmail.com (J.M.P.G.);

8 laranavesalegre@gmail.com (L.N.A.); toni@umh.es (J.A.S.Z.); esebgo@gmail.com

9 (E.S.G).

10 *Corresponding author: adrian.orihuela89@gmail.com

11

12

13 **Abstract**

14 Despite the essential role that vertebrate scavengers play in the ecosystem, most
15 studies have been conducted in Europe and North America, exacerbating the lack of
16 information on vertebrate scavengers in vast regions of the world. Our aim was to
17 describe the functioning and composition of the unknown vertebrate scavenger
18 assemblage in the Gobi Desert, Mongolia, and determine how carcass size and habitat
19 type affect species composition and carrion use. We monitored carcasses with automatic
20 cameras and we also conducted observation points to survey the raptor community and
21 identify the proportion of raptor species making use of the carcasses. We recorded eight
22 vertebrate scavenger species (five birds and three mammals) by camera trapping and
23 seven raptors at observation points. Over half of the raptor species recorded at the
24 observation points were also found feeding on carrion. We found differences in the
25 composition of the avian assemblages between habitat types, where the two most
26 threatened species were only recorded in the mountain habitat. Furthermore, scavenger
27 abundance and consumption rates were higher in large carcasses. This study highlights
28 the importance of scavenging for raptors, of mountains as wildlife refuges, and of
29 vertebrate scavengers for carrion elimination in ecosystems with extreme climatic
30 conditions.

31

32 **Keywords:** Arid ecosystem; Carrion; Consumption rate; Seminomadic herder; Species
33 richness; Vulture

34

35 1. Introduction

36 Vertebrate scavengers play a key role in nutrient cycling, biodiversity
37 maintenance, and disease control (Barton et al., 2013; Beasley et al., 2019), affecting
38 45% of trophic links worldwide (Wilson and Wolkovich, 2011). Thus, the disruption of
39 scavenger assemblages may trigger major mismatches in ecosystems, which can
40 severely affect humans (Markandya et al., 2008). For example, a decrease in the Indian
41 vulture population by 97-99% in less than two decades, resulted in an increase in free-
42 ranging dogs (*Canis lupus familiaris*) and rats (*Rattus sp.*), and consequently in human
43 rabies infections, which costed the Indian government \$34 billion (Markandya et al.,
44 2008; Prakash et al., 2007). However, humans continue to undermine biodiversity. For
45 example, Sebastián-González et al. (2019, 2020) showed that human activity is the main
46 process reducing species richness and network structure of terrestrial vertebrate
47 scavenger communities in a global scale, which may involve an invaluable social,
48 economic and ecological cost.

49 Scavenging dynamics are affected by both biotic and abiotic factors (Barton et
50 al., 2013; DeVault et al., 2004; Wilson and Wolkovich, 2011), being carrion features
51 among the most important ones. Olson et al. (2016) showed that carcass type (i.e., the
52 carrion species) affected the vertebrate scavenger assemblage more than habitat
53 connectivity. Some vertebrate scavenger species (particularly mammalian carnivores)
54 were also found to avoid feeding on conspecific carcasses, leading to carrion
55 partitioning amongst vertebrate and invertebrate scavengers (Moleón et al., 2017).
56 Besides, Moleón et al. (2015) concluded that larger carcasses had higher vertebrate
57 scavenger species richness and consumption rates than the smaller ones. Habitat
58 features can also influence detection times and the composition of the scavenger
59 assemblage feeding on carrion (Pardo-Barquín et al., 2019; Selva et al., 2005). For

60 example, Turner et al. (2017) found that carrion detection times were 50% larger in
61 habitats with more vegetation cover, especially during the warm season. In addition,
62 vegetation cover can influence species composition, with species with developed sense
63 of smell appearing in areas with more cover rather than species more dependent on
64 visual cues (Byrne et al., 2019). Also, birds are expected to occur more often in open
65 than in dense forest areas, where mammals tend to be more abundant (Pardo-Barquín et
66 al., 2019).

67 As happens with other vertebrate groups (Amano et al., 2016; Orihuela-Torres et
68 al., 2020), there are spatial gaps in the knowledge about vertebrate scavenger
69 assemblages worldwide. The vast majority of studies focused on North America and
70 Europe, and to a lesser extent, on Australia and Southern Africa (Sebastián-González et
71 al., 2019, 2020). However, there is a lack of surveys in South America and Asia, which
72 are priority areas both for vultures (obligate scavengers) and raptors (facultative
73 scavengers) due to the high number of species and their threat degree (Buechley et al.,
74 2019). Asia, despite being the largest continent, is probably the least studied in terms of
75 scavenger assemblages. There are only such studies in temperate forests in Japan
76 (Inagaki et al., 2020; Sugiura et al., 2013; Sugiura and Hayashi, 2018) and China
77 (Huang et al., 2014), tropical dry deciduous forests in India (Samson and Ramakrishnan,
78 2017), and tropical rainforests in Borneo (Lim, 2015). Furthermore, there is a noticeable
79 gap in the study of biomes with extreme climatic conditions, such as deserts (Sebastián-
80 González et al., 2019). Our study is located in the pristine great steppe of Mongolia, in
81 the Gobi Desert, an understudied ecosystem which holds high biodiversity values. For
82 instance, this is the one of the most important breeding and migratory area for some
83 endangered raptors (Dixon et al., 2015; Gombobaatar et al., 2012). The great steppe of
84 the Gobi Desert is not homogeneous, combining wide plain steppes scattered with

85 mountains. These mountains act as "vertical islands" in the landscape, increasing
86 microhabitat heterogeneity and providing refuge for wildlife as nesting places, areas to
87 hide from predators or to shelter from the weather (Rixen and Rolando, 2013).

88 Extensively managed livestock production by seminomadic herders is the major
89 socioeconomic activity in Mongolia (Angerer et al., 2008) and these socio-ecological
90 systems are highly relevant for the conservation of scavengers elsewhere (Morales-
91 Reyes et al., 2018).

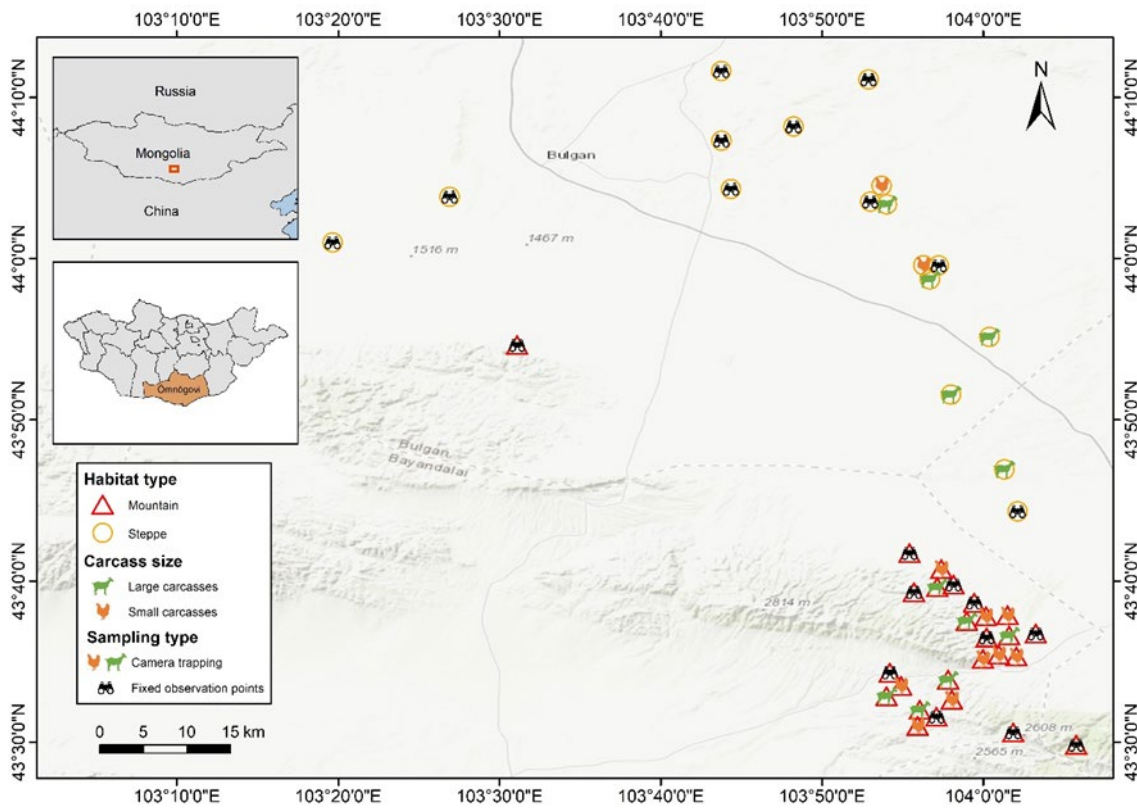
92 The main objective of our study was to identify the functioning and composition
93 of the vertebrate scavenger assemblage in the Gobi Desert in Mongolia. We also studied
94 whether this assemblage is affected by carcass features or habitat type. To do so, we
95 compared the scavenger species composition and the scavenging efficiency of the
96 vertebrate scavenger assemblage in the Gobi Desert between I) habitat types (steppe vs
97 mountain) and II) carcass sizes (large vs small carcasses). We hypothesized that both
98 habitat type and carcass size would affect the composition of the vertebrate scavenger
99 assemblage and, therefore, its scavenging efficiency. Due to the greater heterogeneity of
100 microhabitats in the mountains and the higher amount of carrion in larger carcasses, we
101 predict that both mountain habitat type and large carcasses will have a higher richness
102 and abundance of scavengers and higher carrion consumption rates. III) We also wanted
103 to evaluate the relative use of carrion for the important Mongolian raptor guild. To do
104 so, we compared the avian community (raptors and corvids) observed at fixed
105 observation points with the avian scavenger community detected at carcasses using
106 camera traps. IV) Finally, we compared the species richness and carrion use with that of
107 other vertebrate scavenger assemblages worldwide. We expect low species richness and
108 carrion use in our study area due to the extreme climatic conditions.

109

110 2. Material and methods

111 2.1 Study area

112 Our study area was located in the central Gobi Desert (southern Mongolia; 43°
113 56' N, 103° 44' E; Fig. 1), in the Ömnögovi aimag (province), close to the cities of
114 Dalanzadgad and Bulgan.



115
116 **Fig. 1.** (1.5 column fitting image). Map of the study area in the Ömnögovi aimag
117 (province) in the Gobi Desert, Mongolia. We show the locations of 22 carcasses with
118 different sizes (large vs small) to detect the vertebrate scavenger assemblage and 21
119 fixed observation points in two habitat types (mountain vs steppe).

120 The area has huge temperature contrasts reaching 40°C in summer and -49°C in
121 winter. The mean annual temperature is 4.3°C and the mean annual rainfall is 125 mm
122 (Pfeiffer et al., 2003) with 85–90% of the total annual precipitation falling from April
123 through September. The Gobi Desert is not constant in terms of climate and vegetation,

124 as it is more arid and dry in the center and increases in rainfall and vegetation towards
125 its boundaries (Yu et al., 2004). Our study area was dominated by steppes with rolling
126 topography and scattered mountain ranges with elevations ranging from 706 to 2,825 m
127 a.s.l. (Begzsuren et al., 2004). The Gobi steppe is one of the largest steppes in the world,
128 which has been exploited by nomadic shepherds for millennia, being one of the least
129 populated and well preserved regions in the world.

130

131 2.2 Data sampling

132 In July 2019, we monitored 22 carcasses with automatic cameras activated by
133 movement (model: Browning Strike Force pro HD) to study the vertebrate scavenger
134 assemblage in the Gobi Desert. We used two sizes of fresh carcasses: 1) large, i.e.,
135 domestic goats (*Capra hircus*) weighing between 8.5 - 55 kg (n = 11), and 2) small, i.e.,
136 chickens (*Gallus gallus*) weighing between 0.1 - 0.4 kg (n = 11). Carcasses were placed
137 in two types of habitat: 1) mountain (n = 15) and 2) steppe (n = 7). They were randomly
138 placed at least 500 m apart (small carcasses minimum distance = 600 m; large carcasses
139 minimum distance = 3,150 m) to consider each sample as independent. Carcasses came
140 from local shepherds and were fixed to the ground by stakes to prevent them from being
141 taken out of camera range by scavengers. They were placed equally in the morning and
142 evening. We installed two automatic cameras per carcass. One camera was programmed
143 to take two pictures every 30 seconds with a 30-second delay, while the other took one-
144 minute long videos with a two-minute delay, when motion was detected. First, we
145 checked the photos to identify all vertebrate scavengers (i.e., carrion-consuming) at each
146 monitored carcass. Then, we visualized the videos to avoid possible failures in species
147 detection or identification (see Appendix 1 for detailed information).

148 Moreover, we conducted 21 fixed observation points to determine the avian
149 community (raptors and corvids) at the same time than the carcass monitoring. They
150 were carried out by experienced observers using binoculars and a scope, following
151 methods employed in similar surveys (Sánchez-Zapata et al., 2007). All raptor and
152 corvid species were identified and counted. Fixed observation points were divided into:
153 1) mountain (n = 11) and 2) steppe (n = 10). They lasted 30 min each, and were carried
154 out between 8:30h and 12:30h local time with a minimum distance of 1,500 m
155 (minimum mean distance = 6,500 m) between them (Appendix 1).

156

157 [2.3. Scavenging measures](#)

158 We used four variables to characterize the scavenger assemblage and scavenging
159 efficiency: 1- ‘Richness’ (i.e., total number of vertebrate scavenger species recorded
160 consuming carrion in each carcass or observed in each fixed observation point).
161 Richness was calculated for all vertebrates, and for birds and mammals separately; 2-
162 ‘abundance’ (i.e., maximum number of unequivocally different individuals recorded in
163 a sampling point, i.e., each carcass or fixed observation point). In the case of the
164 carcasses, it was calculated by counting the highest number of individuals appearing
165 simultaneously on a picture (Sebastián-González et al., 2019), as well as individuals
166 who can be differentiated due to age, sex or body features; 3- ‘detection time’ (i.e., time
167 elapsed since the carcass was placed until it is detected by a vertebrate scavenger); 4-
168 ‘consumption rate’ (i.e., amount of carrion consumed at the end of the experiment (kg)
169 divided by consumption time (h)). We also identified the conservation status of each
170 recorded species according to the International Union for Conservation of Nature’s red
171 list of Threatened Species (IUCN, 2020).

172 Finally, we compiled the vertebrate scavenger species richness and carcass
173 consumption rates from scavenger assemblages in the literature with small (ranging 0.2-
174 2 kg) and large carcasses (10-55 kg) worldwide (Sebastián-González et al., 2020) to
175 compare those values with those obtained in our study area (see Appendix 2 for
176 information on these surveys).

177

178 2.4. Statistical analyses

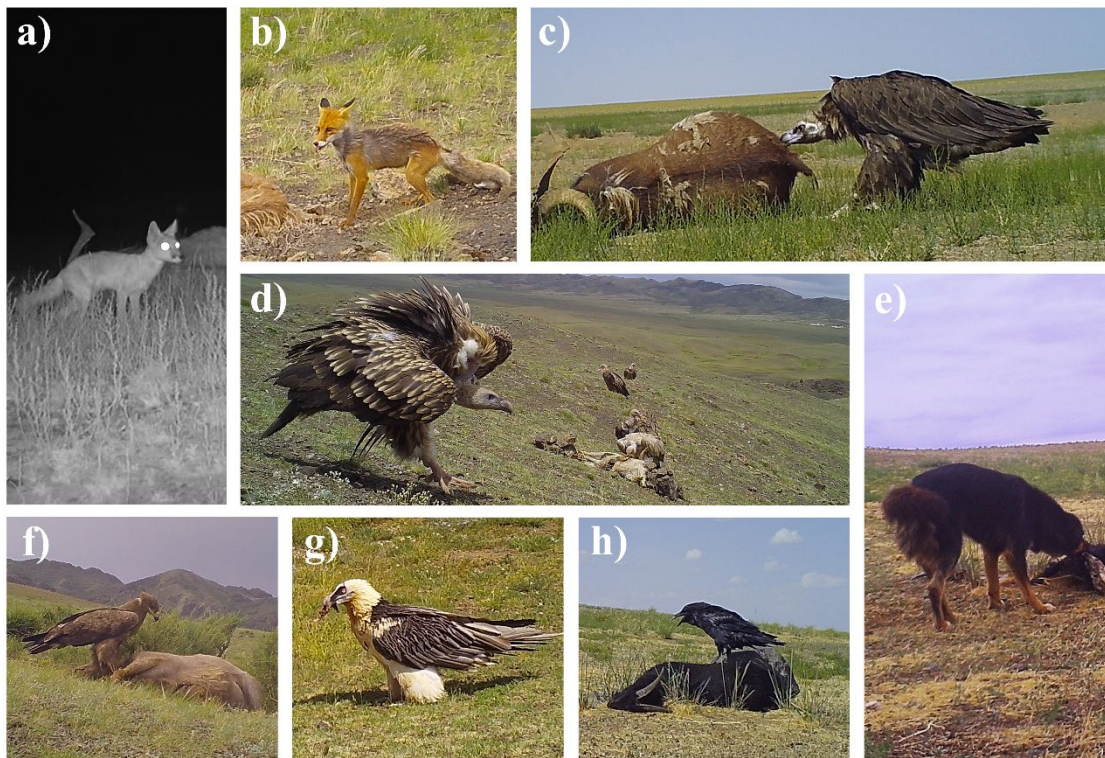
179 To evaluate the differences in vertebrate scavenger assemblages, we used
180 generalized linear models (GLMs) in R 3.6.0 (R Core Team, 2019). In GLMs,
181 ‘richness’, ‘abundance’, ‘detection time’ and ‘consumption rate’ were the response
182 variables, whereas ‘habitat type’ (steppe or mountain), ‘carcass size’ (large or small)
183 and ‘sampling type’ (camera trapping or fixed observation point) were categorical
184 predictors. We used one-predictor GLMs to compare the differences between
185 categorical predictors. In ‘habitat type’ and ‘sampling type’, we only used the avian
186 assemblage for ‘richness’ and ‘abundance’ since in fixed observation point only the
187 avian community (raptors and corvids) was noted, whilst for ‘carcass size’ we compare
188 the total scavenger assemblage (avian and mammals). We used Poisson error
189 distribution for ‘richness’, negative binomial error distribution for ‘abundance’, and
190 Gaussian error distribution for ‘detection time’ and ‘consumption rate’. ‘Detection time’
191 and ‘consumption rate’ were log-transformed to meet normality. Moreover, we
192 compared the vertebrate scavenger assemblages between ‘habitat type’, ‘sampling type’
193 and ‘carcass size’, separately, using the permutational multivariate analysis of variance
194 (PERMANOVA). PERMANOVA is a non-parametric test to analyze differences in the
195 composition and/or relative abundances of organisms of different species in samples
196 from different groups (Anderson, 2001). We also evaluated the dispersion of the

197 communities by means of a PERMADISP analysis. For both PERMANOVA and
198 PERMADISP analyses we used the *vegan* (Oksanen et al., 2019) package in R. We
199 compared avian assemblages between ‘habitat type’ and ‘sampling type’, and the
200 vertebrate scavenger assemblage (birds and mammals) between ‘carcass size’. In
201 addition, we calculated the species accumulation curves to test whether the sampling
202 effort has been sufficient to identify all vertebrate scavenger and raptor species.

203

204 3. Results

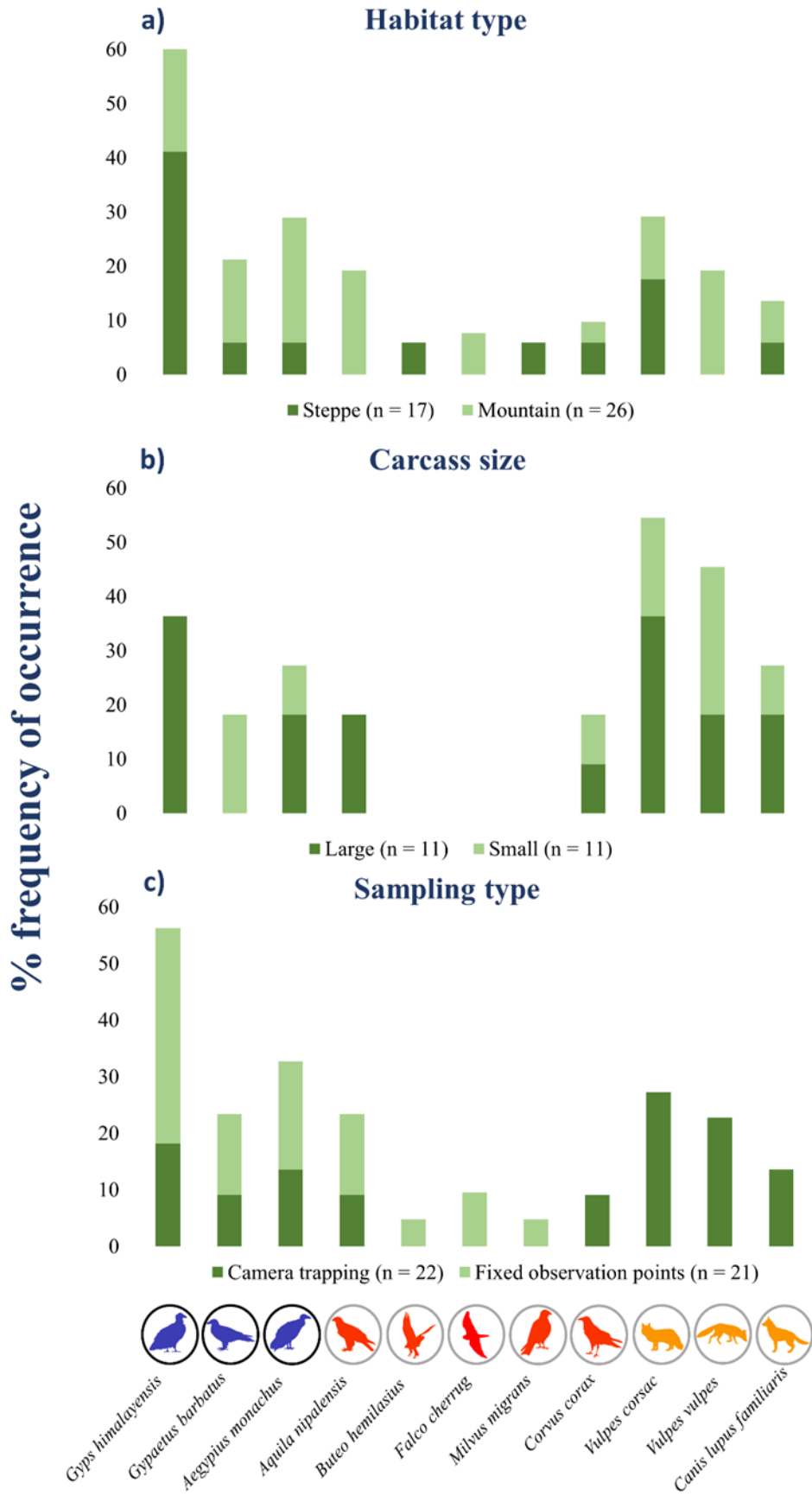
205 We recorded eight vertebrate scavenger species (Table 1; Fig. 2)
206 including three obligate scavengers (i.e., vultures): Himalayan griffons (*Gyps*
207 *himalayensis*), cinereous vultures (*Aegypius monachus*) and bearded vultures (*Gypaetus*
208 *barbatus*), and five facultative scavengers (one raptor, one corvid and three mammalian
209 carnivores; Fig. 3).



210

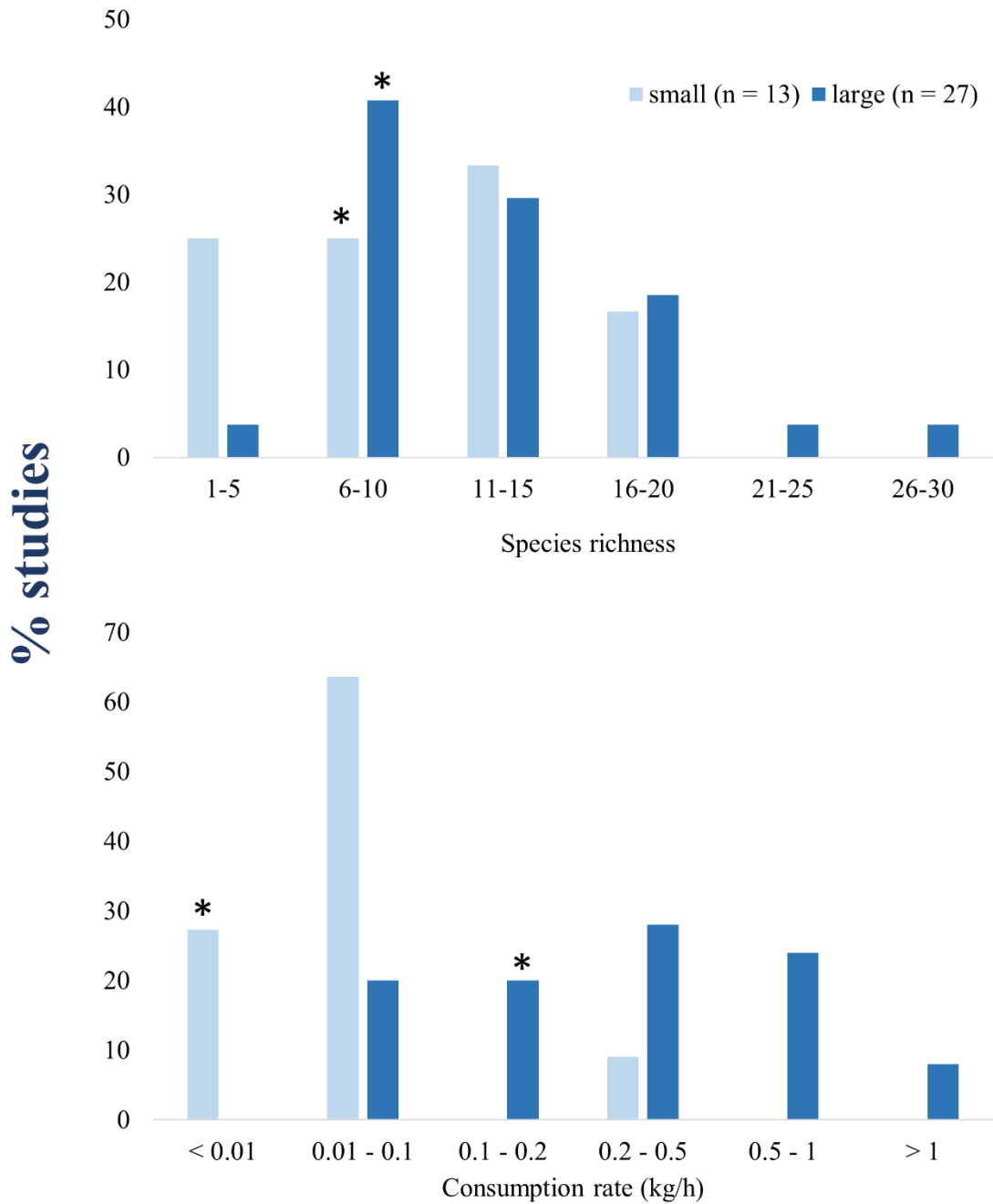
211 **Fig. 2.** (2 column fitting image). All recorded vertebrate scavenger species in our survey
212 in the Gobi Desert, Mongolia. The pictures are organized from the species that appeared
213 in more carcasses (a) to the one that appeared in less carcasses (h). a) corsac fox, b) red
214 fox, c) cinereous vulture, d) Himalayan griffons, e) free-ranging dog, f) steppe eagle, g)
215 bearded vulture and h) common raven.

216 In addition, we detected some additional mammalian carnivores with camera traps,
217 but they did not consumed any carcass, such as the grey wolf (*Canis lupus*) or the
218 marbled polecat (*Vormela peregusna*). Of the five avian scavenger species, 20% were
219 classified as Endangered and 60% as Near Threatened, whereas the three mammalian
220 species were classified as Least Concern (Table 1). The species accumulation curves
221 showed that sampling effort was satisfactory to identify the vertebrate scavenger species
222 of the study area (Appendix 3: Figure 1). Vertebrate scavenging activity was detected at
223 68% (n = 15) of the carcasses, 18% (n = 4) of the carcasses were only consumed by
224 invertebrates and 14% (n = 3) remained unconsumed at the end of the experiment.
225 Mammals scavenged on 55% (n = 12) of the carcasses, and birds on 41% (n = 9) of
226 them. The species that appeared on more carcasses were the corsac fox (*Vulpes corsac*)
227 and the red fox (*Vulpes vulpes*) (Fig. 3; Appendix 3: Table 1 for detailed values).



229 **Fig. 3.** (1 column fitting image). Frequency of occurrence of the vertebrate scavenger
230 assemblage in the Gobi Desert, Mongolia. We compared the frequency of occurrence of
231 each recorded species between: a) habitat type (method: camera trapping and fixed
232 observation point), b) carcass size (method: camera trapping) and c) sampling type
233 (method: camera trapping and fixed observation point). At fixed observation points we
234 only recorded the raptor community, not mammals. Obligate scavengers (black circle)
235 are in blue, facultative scavengers (grey circle) including avian (in red) and mammal
236 scavengers (in orange). See Appendix 3: Table 1 for detailed values.

237 However, the most abundant species was the Himalayan griffon followed by the
238 cinereous vulture (Table 1). Mammals were the first to detect the carrion in most cases
239 (73.3%). Species richness and consumption rate in the Gobi Desert were lower than
240 those in most vertebrate scavenger studies from other regions (Fig. 4).



241

242 **Fig. 4.** (1 column fitting image). Species richness and consumption rate from vertebrate
 243 scavenger surveys worldwide. Bars show the percentage of studies belonging to the
 244 value where they are located. Asterisk represent observed values for small and large
 245 carcasses in our study area.

246

247 We recorded seven raptor species at fixed observation points, including three
248 obligate scavengers (vultures) and four facultative scavengers (other raptors), but we did
249 not record corvids (Table 1). The species accumulation curves showed that most raptor
250 species had been recorded, although it did not reach the asymptote (Appendix 3: Figure
251 1).

252

253 3.1 Habitat type

254 The composition of the avian assemblages was different between steppe and
255 mountain habitats (Appendix 3: Table 2). Total species number (at carcasses and fixed
256 observation points) was slightly higher in the mountain habitat (n = 9) than in the steppe
257 (n = 8), whereas the difference was greater when we compared only the species at the
258 carcasses (n = 8 mountain, n = 4 steppe). In addition, the number of mammal species
259 was higher in the mountain (Table 1). Although all obligate scavengers were recorded in
260 the two habitats, several facultative scavengers only appeared in one (Table 1). We
261 found no significant differences in richness or abundance per sampling point (carcasses
262 and fixed observation points) between the two habitat types (Table 2). In the mountain,
263 the species that appeared in more carcasses was the red fox (33.3%). At the steppe, the
264 corsac fox was present in almost half of the carcasses (42.9%; Fig. 3). We also found no
265 significant difference between detection time and consumption rate between habitat
266 types (Table 2).

267

268 3.2 Carcass size

269 We found no differences in species composition of vertebrate scavenger
270 assemblages between carcass sizes (Appendix 3: Table 2). Vertebrate scavenger species

271 richness was similar in large (n = 7 species) and small carcasses (n = 6). All recorded
272 mammals appeared in both carcass sizes. Cinereous vultures and steppe eagles (*Aquila*
273 *nipalensis*) were only recorded in large carcasses, while bearded vultures only appeared
274 in small carcasses (Table 1). There were no significant differences in species richness
275 per carcass between carcass sizes. However, there were significant differences in
276 abundance per carcass, being four times higher in large than in small carcasses (Table
277 2). Although we found no significant differences in detection time, the consumption rate
278 was much higher in large than in small carcasses (Table 2). The species that were
279 recorded in most of the large carcasses were corsac foxes (36.4%) and cinereous
280 vultures (36.4%), whilst at small carcasses were red foxes (27.3%; Fig. 3). Nonetheless,
281 the most abundant species at large carcasses was the Himalayan griffon whereas it was
282 the red fox at small carcasses (Table 1).

283

284 3.3 Sampling type

285 We found no differences in composition of avian assemblages recorded at
286 monitored carcasses by camera trapping and fixed observation points (Appendix 3:
287 Table 2). The number of avian species recorded by fixed observation points was higher
288 than at automatic cameras (Table 1). We identified 57% of the species recorded at fixed
289 observation points, feeding on carcasses. Furthermore, we found no significant
290 differences in avian species richness or abundance per sampling point (carcass or fixed
291 observation point) between sampling types. All obligate scavengers (i.e., vultures) were
292 recorded by both sampling methods, but we found different species of facultative avian
293 scavengers (Table 1). The most abundant avian species were Himalayan griffons
294 followed by cinereous vultures both at monitored carcasses and fixed observation points
295 (Table 1).

296

297 4. Discussion

298 Some regions of the planet are much less studied than others from a community
299 approach, biasing our understanding about how they affect large-scale processes
300 involving the ecosystems and species that inhabit them (Sebastián-González et al.,
301 2019). Our study presents the first description of the vertebrate scavenger assemblage in
302 the Gobi Desert, Mongolia. This assemblage is mainly composed by avian species
303 (62.5%), which were pervasive and also more abundant at the carcasses than mammals,
304 unlike other arid ecosystems in Africa and Australia, where top carnivores were the
305 main scavengers (Cunningham et al., 2018; Moleón et al., 2015). However, mammals
306 discovered most carcasses and scavenged in a high number of them, revealing the key
307 role they play in carrion removal. Top carnivores like grey wolves were detected in the
308 study area, but were not found feeding on the carcasses, maybe because Eurasian top
309 predators have a long history of persecution (Ordiz et al., 2013). Furthermore, we found
310 differences in avian species composition (raptors and corvids) between mountain and
311 steppe, but not between carcass size or habitat type. The two most threatened species,
312 the steppe eagle and the saker falcon (*Falco cherrug*), were only recorded in the
313 mountains, highlighting the importance of these “vertical islands” in landscapes such as
314 steppes where there is a lack of wildlife refuge and nesting places.

315 Steppes are ecosystems with very extreme conditions that constrain the presence of
316 many species (Currie et al., 2004), including scavengers. Consequently, we recorded a
317 lower number of vertebrate scavenger species than in most study areas worldwide,
318 further considering that our study area was located in a well-preserved ecosystem.
319 However, other studies conducted in steppes of Argentina (Sebastián-González et al.,
320 2013; Travaini et al., 1998) and Australia (Read and Wilson, 2004) showed between 5-9

321 vertebrate scavenger species, similar to our study. These results support the hypothesis
322 that vertebrate scavenger diversity is lower in ecosystems with more extreme climatic
323 conditions (Mateo-Tomás et al., 2015). Furthermore, the mean carcass consumption rate
324 (0.0024 kg/h at small carcasses and 0.194 kg/h at large carcasses) is low compared to
325 other sites. The Mongolian steppe is well known for its large number of livestock,
326 which has doubled in the last decade (NSO, 2020). This livestock availability provides a
327 large amount of carrion biomass, which added to the decrease in vulture populations in
328 Asia (Prakash et al., 2007), may result in a low consumption rate and carrion removal
329 by vertebrate scavengers in this area. These results indicate that invertebrate scavengers
330 may have a relevant role, at least in the warm season (DeVault et al., 2004).

331 It has been shown that larger carcasses facilitate more organized, richer and more
332 abundant vertebrate scavenger assemblages, removing carrion faster (Moleón et al.,
333 2015; Stiegler et al., 2020; Turner et al., 2017). Our results show that carcass size
334 strongly and positively affected the abundance of scavenging vertebrates and their
335 consumption rate. Larger carcasses had a much higher abundance of avian species,
336 especially vultures such as Himalayan griffons and cinereous vultures which were
337 virtually absent at small carcasses, making the consumption rate much higher in larger
338 carcasses (Moleón et al., 2015). Furthermore, although we found no significant
339 differences in vertebrate scavenger species composition between carcass sizes, different
340 species appeared at each of them. For example, the bearded vulture was only recorded at
341 small carcasses, demonstrating a preference for smaller carcasses, as suggested by
342 Moreno-Opo et al. (2015), and the steppe eagle or the cinereous vulture only appeared at
343 large carcasses.

344 At fixed observation points, we recorded seven raptor species, some of them
345 categorized as endangered, such as the saker falcon and the steppe eagle. In addition,

346 some facultative scavenger raptors, such as the black kite (*Milvus migrans*) and upland
347 buzzard (*Buteo hemilasius*), appeared at fixed observation points but were not recorded
348 feeding on carcasses, as happened in Argentinean Patagonia (Travaini et al., 1998). This
349 may be due to different dietary choices, season or competitive interactions (Pereira et
350 al., 2014; Sebastián-González et al., 2016), as the Steppe of Mongolia is rich in
351 micromammals (Dixon et al., 2017) and some species may prefer them to carrion.
352 However, carrion consumption is a strategy used by a large number of raptor species in
353 ecosystems worldwide (Sebastián-González et al., 2020, 2019). Our survey exposed that
354 more than half of recorded raptor species consumed carrion, highlighting the relevance
355 of this food resource in the Gobi Desert food web (Wilson and Wolkovich, 2011).

356 Our findings reveals the, hitherto, unknown vertebrate scavenger assemblage in
357 the Gobi Desert. It also highlights the importance of carrion resource for raptors and the
358 mountains as a wildlife refuge in our study area, which is a key breeding and migratory
359 area for many endangered raptor species. Through this work we aid to fill spatial gaps in
360 order to understand the large-scale processes that affect scavenger assemblages
361 (Sebastián-González et al., 2019), which are especially unknown in desert regions.
362 Finally, it is necessary to highlight the fundamental role of seminomadic extensive
363 livestock systems, particularly in arid regions, in the conservation of vertebrate
364 scavengers and the ecosystem services they provide (Morales-Reyes et al., 2018).

365 **Acknowledgements**

366 AOT, JMPG, ZMR, LNA and ESG were supported by Generalitat Valenciana
367 (SEJI/2018/024), ZMR and LNA also by contracts co-funded by the Generalitat
368 Valenciana and the European Social Fund (APOSTD/2019/016 and ACIF/2019/056,
369 respectively), and JASZ by funds from the Spanish Ministry of Science, Innovation and
370 Universities and the European Regional Development Fund (RTI2018-099609-B-C21).

371

372 **References**

373 Amano, T., Lamming, J.D.L., Sutherland, W.J., 2016. Spatial Gaps in Global
374 Biodiversity Information and the Role of Citizen Science. *Bioscience* 66, 393–400.
375 <https://doi.org/10.1093/biosci/biw022>

376 Anderson, M.J., 2001. A new method for non-parametric multivariate analysis of
377 variance. *Austral Ecol.* 26, 32–46. [https://doi.org/10.1111/j.1442-](https://doi.org/10.1111/j.1442-9993.2001.01070.pp.x)
378 [9993.2001.01070.pp.x](https://doi.org/10.1111/j.1442-9993.2001.01070.pp.x)

379 Angerer, J., Han, G., Fujisaki, I., Havstad, K., 2008. Climate change and ecosystems of
380 Asia with emphasis on inner Mongolia and Mongolia. *Rangelands* 30, 46–51.
381 [https://doi.org/10.2111/1551-501X\(2008\)30\[46:CCAEOA\]2.0.CO;2](https://doi.org/10.2111/1551-501X(2008)30[46:CCAEOA]2.0.CO;2)

382 Barton, P.S., Cunningham, S.A., Lindenmayer, D.B., Manning, A.D., 2013. The role of
383 carrion in maintaining biodiversity and ecological processes in terrestrial
384 ecosystems. *Oecologia*. <https://doi.org/10.1007/s00442-012-2460-3>

385 Beasley, J.C., Olson, Z.H., Selva, N., DeVault, T.L., 2019. Ecological Functions of
386 Vertebrate Scavenging, in: *Carrion Ecology and Management, Wildlife Research*
387 *Monographs* 2. Springer, Cham, pp. 125–157. [https://doi.org/10.1007/978-3-030-](https://doi.org/10.1007/978-3-030-16501-7_6)
388 [16501-7_6](https://doi.org/10.1007/978-3-030-16501-7_6)

389 Begzsuren, S., Ellis, J.E., Ojima, D.S., Coughenour, M.B., Chuluun, T., 2004. Livestock
390 responses to droughts and severe winter weather in the Gobi Three Beauty
391 National Park, Mongolia. *J. Arid Environ.* 59, 785–796.
392 <https://doi.org/10.1016/j.jaridenv.2004.02.001>

393 Buechley, E.R., Santangeli, A., Girardello, M., Neate-Clegg, M.H.C., Oleyar, D.,

394 McClure, C.J.W., Şekercioğlu, Ç.H., 2019. Global raptor research and
395 conservation priorities: Tropical raptors fall prey to knowledge gaps. *Divers.*
396 *Distrib.* 25, 856–869. <https://doi.org/10.1111/ddi.12901>

397 Byrne, M.E., Holland, A.E., Turner, K.L., Bryan, A.L., Beasley, J.C., 2019. Using
398 multiple data sources to investigate foraging niche partitioning in sympatric
399 obligate avian scavengers. *Ecosphere* 10, e02548.
400 <https://doi.org/10.1002/ecs2.2548>

401 Cunningham, C.X., Johnson, C.N., Barmuta, L.A., Hollings, T., Woehler, E.J., Jones,
402 M.E., 2018. Top carnivore decline has cascading effects on scavengers and carrion
403 persistence. *Proc. R. Soc. B Biol. Sci.* 285, 20181582.
404 <https://doi.org/10.1098/rspb.2018.1582>

405 Currie, D.J., Mittelbach, G.G., Cornell, H. V., Field, R., Guégan, J.F., Hawkins, B.A.,
406 Kaufman, D.M., Kerr, J.T., Oberdorff, T., O'Brien, E., Turner, J.R.G., 2004.
407 Predictions and tests of climate-based hypotheses of broad-scale variation in
408 taxonomic richness. *Ecol. Lett.* 7, 1121–1134. [https://doi.org/10.1111/j.1461-](https://doi.org/10.1111/j.1461-0248.2004.00671.x)
409 [0248.2004.00671.x](https://doi.org/10.1111/j.1461-0248.2004.00671.x)

410 DeVault, T.L., Brisbin, I.L., Rhodes, O.E., 2004. Factors influencing the acquisition of
411 rodent carrion by vertebrate scavengers and decomposers. *Can. J. Zool.* 82, 502–
412 509. <https://doi.org/10.1139/z04-022>

413 Dixon, A., Ming, M., Batbayar, N., 2015. Importance of the Qinghai-Tibetan plateau for
414 the Endangered Saker Falcon *Falco cherrug*. *Forktail* 37–42.

415 Dixon, A., Rahman, M.L., Galtbalt, B., Gunga, A., Sugarsaikhan, B., Batbayar, N.,
416 2017. Avian electrocution rates associated with density of active small mammal
417 holes and power-pole mitigation: Implications for the conservation of Threatened

418 raptors in Mongolia. *J. Nat. Conserv.* 36, 14–19.
419 <https://doi.org/10.1016/j.jnc.2017.01.001>

420 Gombobaatar, S., Yosef, R., Odkhuu, B., Sumiya, D., 2012. Breeding ecology of the
421 Steppe Eagle (*Aquila nipalensis*) in Mongolia. *Ornis Mongolica* 1, 13–19.

422 Huang, Z.P., Qi, X.G., Garber, P.A., Jin, T., Guo, S.T., Li, S., Li, B.G., 2014. The use of
423 camera traps to identify the set of scavengers preying on the carcass of a golden
424 snub-nosed monkey (*Rhinopithecus roxellana*). *PLoS One* 9, e87318.
425 <https://doi.org/10.1371/journal.pone.0087318>

426 Inagaki, A., Allen, M.L., Maruyama, T., Yamazaki, K., Tochigi, K., Naganuma, T.,
427 Koike, S., 2020. Vertebrate scavenger guild composition and utilization of carrion
428 in an East Asian temperate forest. *Ecol. Evol.* 10, 1223–1232.
429 <https://doi.org/10.1002/ece3.5976>

430 IUCN, 2020. IUCN Red List of Threatened Species [WWW Document]. URL
431 <https://www.iucnredlist.org/> (accessed 4.16.20).

432 Lim, N.T.L., 2015. Scavengers and Carcass Removal in Tropical Southeast Asia.
433 ProQuest Diss. Theses. DISSERTATION.

434 Markandya, A., Taylor, T., Longo, A., Murty, M.N., Murty, S., Dhavala, K., 2008.
435 Counting the cost of vulture decline-An appraisal of the human health and other
436 benefits of vultures in India. *Ecol. Econ.* 67, 194–204.
437 <https://doi.org/10.1016/j.ecolecon.2008.04.020>

438 Mateo-Tomás, P., Olea, P.P., Moleón, M., Vicente, J., Botella, F., Selva, N., Viñuela, J.,
439 Sánchez-Zapata, J.A., 2015. From regional to global patterns in vertebrate
440 scavenger communities subsidized by big game hunting. *Divers. Distrib.* 21, 913–

441 924. <https://doi.org/10.1111/ddi.12330>

442 Moleón, M., Martínez-Carrasco, C., Muellerklein, O.C., Getz, W.M., Muñoz-Lozano,
443 C., Sánchez-Zapata, J.A., 2017. Carnivore carcasses are avoided by carnivores. *J.*
444 *Anim. Ecol.* 86, 1179–1191. <https://doi.org/10.1111/1365-2656.12714>

445 Moleón, M., Sánchez-Zapata, J.A., Sebastián-González, E., Owen-Smith, N., 2015.
446 Carcass size shapes the structure and functioning of an African scavenging
447 assemblage. *Oikos* 124, 1391–1403. <https://doi.org/10.1111/oik.02222>

448 Morales-Reyes, Z., Martín-López, B., Moleón, M., Mateo-Tomás, P., Botella, F.,
449 Margalida, A., Donazar, J.A., Blanco, G., Pérez, I., Sánchez-Zapata, J.A., 2018.
450 Farmer Perceptions of the Ecosystem Services Provided by Scavengers: What,
451 Who, and to Whom. *Conserv. Lett.* 11, e12392. <https://doi.org/10.1111/conl.12392>

452 Moreno-Opo, R., Trujillano, A., Margalida, A., 2015. Optimization of supplementary
453 feeding programs for European vultures depends on environmental and
454 management factors. *Ecosphere* 6, art127. <https://doi.org/10.1890/es15-00009.1>

455 NSO, 2020. NSO (National Statistical Office). [WWW Document]. URL
456 http://1212.mn/Stat.aspx?LIST_ID=976_L10_1&type=description (accessed
457 6.3.20).

458 Oksanen, J., Blanchet, F.G., Friendly, M., Kindt, R., Legendre, P., Mcglinn, D.,
459 Minchin, P.R., O’hara, R.B., Simpson, G.L., Solymos, P., Henry, M., Stevens, H.,
460 Szoecs, E., Maintainer, H.W., 2019. Package “vegan” Title Community Ecology
461 Package.

462 Olson, Z.H., Beasley, J.C., Rhodes, O.E., 2016. Carcass type affects local scavenger
463 guilds more than habitat connectivity. *PLoS One* 11, e0147798.

464 <https://doi.org/10.1371/journal.pone.0147798>

465 Ordiz, A., Bischof, R., Swenson, J.E., 2013. Saving large carnivores, but losing the apex
466 predator? *Biol. Conserv.* 168, 128–133.
467 <https://doi.org/10.1016/j.biocon.2013.09.024>

468 Orihuela-Torres, A., Tinoco, B., Ordóñez-Delgado, L., Espinosa, C.I., 2020. Knowledge
469 Gaps or Change of Distribution Ranges? Explaining New Records of Birds in the
470 Ecuadorian Tumbesian Region of Endemism. *Diversity* 12, 66.
471 <https://doi.org/10.3390/d12020066>

472 Pardo-Barquín, E., Mateo-Tomás, P., Olea, P.P., 2019. Habitat characteristics from
473 local to landscape scales combine to shape vertebrate scavenging communities.
474 *Basic Appl. Ecol.* 34, 126–139. <https://doi.org/10.1016/j.baae.2018.08.005>

475 Pereira, L.M., Owen-Smith, N., Moleón, M., 2014. Facultative predation and
476 scavenging by mammalian carnivores: Seasonal, regional and intra-guild
477 comparisons. *Mamm. Rev.* 44, 44–55. <https://doi.org/10.1111/mam.12005>

478 Pfeiffer, M., Chimedregzen, L., Ulykpan, K., 2003. Community organization and
479 species richness of ants (Hymenoptera/ Formicidae) in Mongolia along an
480 ecological gradient from steppe to Gobi desert. *J. Biogeogr.* 30, 1921–1935.
481 <https://doi.org/10.1046/j.0305-0270.2003.00977.x>

482 Prakash, V., Green, R., Pain, D., Ranade, S., Saravanan, S., Prakash, N.,
483 Venkitachalam, R., Cuthber, R., Rahmani, A., Cunningham, A., 2007. Recent
484 Changes in Populations of Resident *Gyps* Vultures in India. *J. Bombay Nat. Hist.*
485 *Soc.* 104, 127–133.

486 R Core Team, R., 2019. R: A language and environment for statistical computing. R

487 Foundation for Statistical Computing. R version 3.6. 0.

488 Read, J.L., Wilson, D., 2004. Scavengers and detritivores of kangaroo harvest offcuts in
489 arid Australia. *Wildl. Res.* 31, 51–56. <https://doi.org/10.1071/WR02051>

490 Rixen, C., Rolando, A., 2013. The Impacts of Skiing and Related Winter Recreational
491 Activities on Mountain Environments, The Impacts of Skiing and Related Winter
492 Recreational Activities on Mountain Environments. Bentham Science Publishers,
493 USA. <https://doi.org/10.2174/97816080548861130101>

494 Samson, A., Ramakrishnan, B., 2017. Scavenging Mode of Vertebrate Scavengers on
495 Domestic Buffalos *Bubalus bubalis* (Linnaeus , 1785) Killed by Tiger *Panthera*
496 *tigris* and Natural Deaths in Southern India. *Podoces* 12, 22–26.

497 Sánchez-Zapata, J.A., Donázar, J.A., Delgado, A., Forero, M.G., Ceballos, O., Hiraldo,
498 F., 2007. Desert locust outbreaks in the Sahel: Resource competition, predation and
499 ecological effects of pest control. *J. Appl. Ecol.* 44, 323–329.
500 <https://doi.org/10.1111/j.1365-2664.2007.01279.x>

501 Sebastián-González, E., Barbosa, J.M., Pérez-García, J.M., Morales-Reyes, Z., Botella,
502 F., Olea, P.P., Mateo-Tomás, P., Moleón, M., Hiraldo, F., Arrondo, E., Donázar,
503 J.A., Cortés-Avizanda, A., Selva, N., Lambertucci, S.A., Bhattacharjee, A.,
504 Brewer, A., Anadón, J.D., Abernethy, E., Rhodes, O.E., Turner, K., Beasley, J.C.,
505 DeVault, T.L., Ordiz, A., Wikenros, C., Zimmermann, B., Wabakken, P., Wilmers,
506 C.C., Smith, J.A., Kendall, C.J., Ogada, D., Buechley, E.R., Frehner, E., Allen,
507 M.L., Wittmer, H.U., Butler, J.R.A., du Toit, J.T., Read, J., Wilson, D., Jerina, K.,
508 Krofel, M., Kostecke, R., Inger, R., Samson, A., Naves-Alegre, L., Sánchez-
509 Zapata, J.A., 2019. Scavenging in the Anthropocene: Human impact drives
510 vertebrate scavenger species richness at a global scale. *Glob. Chang. Biol.* 25,

511 3005–3017. <https://doi.org/10.1111/gcb.14708>

512 Sebastián-González, E., Moleón, M., Gibert, J.P., Botella, F., Mateo-Tomás, P., Olea,
513 P.P., Guimarães, P.R., Sánchez-Zapata, J.A., 2016. Nested species- rich networks
514 of scavenging vertebrates support high levels of interspecific competition. *Ecology*
515 97, 95–105. <https://doi.org/10.1890/15-0212.1>

516 Sebastián-González, E., Morales-Reyes, Z., Botella, F., Naves-Alegre, L., Pérez-García,
517 J.M., Mateo-Tomás, P., Olea, P.P., Moleón, M., Barbosa, J.M., Hiraldo, F.,
518 Arrondo, E., Donázar, J.A., Cortés-Avizanda, A., Selva, N., Lambertucci, S.A.,
519 Bhattacharjee, A., Brewer, A.L., Abernethy, E.F., Turner, K.L., Beasley, J.C.,
520 DeVault, T.L., Gerke, H.C., Rhodes, O.E., Ordiz, A., Wikenros, C., Zimmermann,
521 B., Wabakken, P., Wilmers, C.C., Smith, J.A., Kendall, C.J., Ogada, D., Frehner,
522 E., Allen, M.L., Wittmer, H.U., Butler, J.R.A., du Toit, J.T., Margalida, A., Oliva-
523 Vidal, P., Wilson, D., Jerina, K., Krofel, M., KostECKE, R., Inger, R., Per, E.,
524 Ayhan, Y., Ulusoy, H., Vural, D., Inagaki, A., Koike, S., Samson, A., Perrig, P.L.,
525 Spencer, E., Newsome, T.M., Heurich, M., Anadón, J.D., Buechley, E.R., Sánchez-
526 Zapata, J.A., 2020. Network structure of vertebrate scavenger assemblages at the
527 global scale: drivers and ecosystem functioning implications. *Ecography (Cop.)*.
528 *ecog.05083*. <https://doi.org/10.1111/ecog.05083>

529 Sebastián-González, E., Sánchez-Zapata, J.A., Donázar, J.A., Selva, N., Cortés-
530 Avizanda, A., Hiraldo, F., Blázquez, M., Botella, F., Moleón, M., 2013. Interactive
531 effects of obligate scavengers and scavenger community richness on lagomorph
532 carcass consumption patterns. *Ibis (Lond. 1859)*. 155, 881–885.
533 <https://doi.org/10.1111/ibi.12079>

534 Selva, N., Jędrzejewska, B., Jędrzejewski, W., Wajrak, A., 2005. Factors affecting

535 carcass use by a guild of scavengers in European temperate woodland. *Can. J.*
536 *Zool.* 83, 1590–1601. <https://doi.org/10.1139/z05-158>

537 Stiegler, J., von Hoermann, C., Müller, J., Benbow, M.E., Heurich, M., 2020. Carcass
538 introduction for scavenger conservation in a temperate forest ecosystem. *Ecosphere*
539 11, e03063. <https://doi.org/10.1002/ecs2.3063>

540 Sugiura, S., Hayashi, M., 2018. Functional compensation by insular scavengers: the
541 relative contributions of vertebrates and invertebrates vary among islands.
542 *Ecography (Cop.)*. 41, 1173–1183. <https://doi.org/10.1111/ecog.03226>

543 Sugiura, S., Tanaka, R., Taki, H., Kanzaki, N., 2013. Differential responses of
544 scavenging arthropods and vertebrates to forest loss maintain ecosystem function
545 in a heterogeneous landscape. *Biol. Conserv.* 159, 206–213.
546 <https://doi.org/10.1016/j.biocon.2012.11.003>

547 Travaini, A., Donazar, J.A., Rodriguez, A., Ceballos, O., Funes, M., Delibes, M.,
548 Hiraldo, F., 1998. Use of European hare (*Lepus europaeus*) carcasses by an avian
549 scavenging assemblage in Patagonia. *J. Zool.* 246, 175–181.
550 <https://doi.org/10.1111/j.1469-7998.1998.tb00146.x>

551 Turner, K.L., Abernethy, E.F., Conner, L.M., Rhodes, O.E., Beasley, J.C., 2017. Abiotic
552 and biotic factors modulate carrion fate and vertebrate scavenging communities.
553 *Ecology* 98, 2413–2424. <https://doi.org/10.1002/ecy.1930>

554 Wilson, E.E., Wolkovich, E.M., 2011. Scavenging: How carnivores and carrion
555 structure communities. *Trends Ecol. Evol.* 26, 129–135.
556 <https://doi.org/10.1016/j.tree.2010.12.011>

557 Yu, F., Price, K.P., Ellis, J., Feddema, J.J., Shi, P., 2004. Interannual variations of the

558 grassland boundaries bordering the eastern edges of the Gobi Desert in central

559 Asia. *Int. J. Remote Sens.* 25, 327–346.

560 <https://doi.org/10.1080/0143116031000084297>

561

562

Tables

Table 1. Vertebrate scavenger and raptor species richness and abundance for each habitat type (steppe or mountain), carcass size (large or small) and sampling type (camera trapping or fixed point) in the Gobi Desert, Mongolia. We also report for each species, the total abundance (Total), the percentage of scavenged carcasses (% carcasses), and the conservation status of each species according to the IUCN red list of threatened species (Endangered (EN), Least Concern (LC) and Near Threatened (NT)).

	Habitat type		Carcass size		Sampling type		Total	% carcasses	IUCN
	Steppe (n = 17)	Mountain (n = 26)	Large (n = 11)	Small (n = 11)	Camera trapping (n = 22)	Fixed point (n = 21)			
<i>Aegypius monachus</i>	16	14	9	0	9	21	30	18.18	NT
<i>Gypaetus barbatus</i>	1	4	0	2	2	3	5	9.09	NT
<i>Gyps himalayensis</i>	6	59	27	1	28	37	65	13.64	NT
<i>Aquila nipalensis</i>	0	7	3	0	3	4	7	9.09	EN
<i>Buteo hemilasius</i>	2	0	0	0	0	2	2	0	LC
<i>Falco cherrug</i>	0	3	0	0	0	3	3	0	EN
<i>Milvus migrans</i>	1	0	0	0	0	1	1	0	LC
<i>Corvus corax</i>	1	2	1	2	3	0	3	9.09	LC
<i>Vulpes corsac</i>	3	3	4	2	6	-	6	27.27	LC
<i>Vulpes vulpes</i>	0	9	5	4	9	-	9	22.73	LC
<i>Canis lupus familiaris</i>	2	3	4	1	5	-	5	13.64	
Total abundance	32	104	53	12	65	71	156		
Avian species richness	6	6	4	3	5	7	10		
Mammal species richness	2	3	3	3	3	-	3		
Total species richness	8	9	7	6	8	7	13		

Table 2. “Species richness”, “abundance”, “detection time” and “consumption rate” for each habitat type (mountain or steppe) and carcass size (large or small). Values represent mean \pm standard deviation and sample size (n) of the vertebrate scavenger assemblage in the Gobi Desert, Mongolia. The results of univariate generalized linear models (GLMs) are shown, which tested for differences between habitat type and carcass size in terms of ‘species richness’, ‘abundance’, ‘detection time’ and ‘consumption rate’. We show the estimate and the standard error (SE) of the univariate GLMs and the *p*-value. Significant *p*-values are in bold.

	Habitat type					Carcass size				
	Mountain	Steppe	Estimate	SE	<i>p</i> -value	Large	Small	Estimate	SE	<i>p</i> -value
Species richness	1.27 \pm 1.12 (26)	0.94 \pm 0.83 (17)	-0.2257	0.3561	0.526	1.55 \pm 1.12 (11)	0.91 \pm 0.83 (11)	0.5306	0.3985	0.183
Abundance	4.00 \pm 7.96 (26)	1.88 \pm 2.69 (17)	-0.7679	0.5890	0.192	4.82 \pm 10.02 (11)	1.09 \pm 1.04 (11)	1.4854	0.5791	0.010
Detection time (h)	33.38 \pm 25.84 (13)	31.13 \pm 16.92 (6)	-0.0768	0.4237	0.858	29.07 \pm 13.85 (10)	36.66 \pm 29.21 (9)	-0.0689	0.3945	0.863
Consumption rate (kg/h)	0.076 \pm 0.089 (11)	0.042 \pm 0.027 (4)	0.7322	1.2388	0.565	0.12 \pm 0.07(8)	0.004 \pm 0.003(7)	3.7395	0.4031	<0.001

Appendices

Appendix 1. Database used for statistical analysis. For each fixed observation point and/or carcass point we show: start time and date, detection time (h), carcass weight (kg), consumption rate (kg/h), avian richness, avian abundance, mammal richness, mammal abundance, total richness, total abundance and recorded species. The description of each variable is explained in metadata.

Appendix 2. Database that compiles published vertebrate scavenger studies worldwide (Sebastián-González et al., 2020). For each study, we show: citation, country, number of scavenger species, habitat, carcass species, carcass size, carcass weight (kg), consumption rate (kg/h) and reference. The description of each variable is explained in metadata.

Appendix 3: Figure 1. Species accumulation curves and standard error (grey shadow) to measure the sampling effort in order to estimate the vertebrate scavenger (avian and mammals) species richness and raptor species richness of the Gobi Desert, Mongolia. a) Number of carcasses monitored by camera trapping, b) Number of fixed observation points, c) Number of fixed observation points and monitored carcasses.

Appendix 3: Table 1. Frequency of occurrence per species of the vertebrate scavenger assemblage in the Gobi Desert, Mongolia. Results are shown for each habitat type (steppe or mountain), carcass size (large or small) and sampling type (camera trapping or fixed observation point).

Appendix 3: Table 2. Comparison of vertebrate scavenger assemblages of the Gobi Desert, Mongolia, between habitat types (mountain vs steppe), carcass sizes (large vs

small) and sampling types (carcass by camera trapping vs fixed observation point) by means of permutational multivariate analysis of variance (PERMANOVA), and permutational analysis of distance (PERMADIST). We show the Predictor (categorical predictor), Df (degrees of freedom), SS (sum of squares), R2 (pseudo R2), MS (mean of squares), F (pseudo F-statistic) and the p-value. Significant p-values are in bold.