JYX
JYVÄSKYLÄN YLIOPISTO
UNIVERSITY OF JYVÄSKYLÄ

This is a self-archived version of an original article. This version may differ from the original in pagination and typographic details.

Author(s): Naves-Alegre, Lara; Morales-Reyes, Zebensui; Sánchez-Zapata, José Antonio; Sebastián-González, Esther; Ovaskainen, Otso

Title: Scavenging in the realm of senses : smell and vision drive recruitment at carcasses in Neotropical ecosystems

Year: 2022

Version: Accepted version (Final draft)

Copyright: © Authors, 2022

Rights: CC BY 4.0

Rights url: https://creativecommons.org/licenses/by/4.0/

Please cite the original version:

Naves-Alegre, L., Morales-Reyes, Z., Sánchez-Zapata, J. A., Sebastián-González, E., & Ovaskainen, O. (2022). Scavenging in the realm of senses : smell and vision drive recruitment at carcasses in Neotropical ecosystems. Proceedings of the Royal Society B : Biological Sciences, 289(1986), Article 20220843. https://doi.org/10.1098/rspb.2022.0843

This is a previous version of the article published in Proceedings of the Royal Society B: Biological Sciences. 2022, 289: 20220843. https://doi.org/10.1098/rspb.2022.0843

Scavenging in the realm of senses: smell and vision drive recruitment at carcasses in Neotropical ecosystems

Lara Naves-Alegre*[1,2], Zebensui Morales-Reyes[1,3], José Antonio Sánchez-Zapata[1], Esther Sebastián-González[2], Otso Ovaskainen[4,5,6]

[1]Department of Applied Biology, Centro de Investigación e Innovación Agroalimentaria y Agroambiental (CIAGRO-UMH), Miguel Hernández University of Elche, Avinguda de la Universitat d'Elx, s/n, 03202, Elche, Spain.

[2]Departament of Ecology, University of Alicante, Carr. de San Vicente del Raspeig, s/n, 03690, San Vicente del Raspeig, Alicante, Spain.

[3]Instituto de Estudios Sociales Avanzados (IESA), CSIC, Campo Santo de los Mártires, 7, 14004 Córdoba, Spain

[4]Department of Biological and Environmental Science, University of Jyväskylä, P.O. Box 35 (Survontie 9C), FI-40014 Jyväskylä, Finland

[5]Organismal and Evolutionary Biology Research Programme, Faculty of Biological and Environmental Sciences, University of Helsinki, P.O. Box 65, Helsinki 00014, Finland

[6]Department of Biology, Centre for Biodiversity Dynamics, Norwegian University of Science and Technology, Trondheim N-7491, Norway

***Corresponding autor:** Lara Naves-Alegre

+34 618 420 354

e-mail: laranavesalegre@gmail.com

ORCID: 0000-0002-4712-4129

Abstract

Social information, acquired through the observation of other individuals, is especially relevant among species belonging to the same guild. The unpredictable and ephemeral nature of carrion implies that social mechanisms may be selected among scavenger species to facilitate carcass location and consumption. Here, we apply a survival-modelling strategy to data obtained through the placement and monitoring of carcasses in the field to analyse possible information transmission cascades within a Neotropical scavenger community. Our study highlights how the use of different senses (smell and sight) within this guild facilitates carcass location through the transmission of social information between species with different carrion foraging efficiencies. Vultures with a highly developed sense of smell play a key role in this process, as they are the first to arrive at the carcasses and their presence seems to serve as a visual cue for other species to locate the resource. Our study supports the local enhancement hypothesis within scavengers, whereby individuals locate carcasses by following foraging heterospecifics, also suggesting the importance of the sense of smell in the maintenance of the community structure.

Keywords

Foraging behaviour; intra-guild interactions; interspecific communication; public information transmission; scavenging assemblages; species networks

Introduction

Social information refers to the acquisition of cues by monitoring how other individuals interact with the environment [1]. The use of this kind of information is increasingly recognized as a widespread phenomenon in biology [2,3]. Social information transmission is known to influence animal movement [4], foraging patterns [5], habitat selection and reproduction [6]. Traditionally, social information was understood to occur between individuals belonging to the same species (i.e., conspecifics) since they share their ecological needs [7]. Later on, information transmission processes have also become evident between individuals of different species (i.e., heterospecifics) that share and compete for a resource [8,9]. While most studies

50 have focused on information exchanges among conspecifics, fewer have analysed social
51 facilitation between species from the same guild, where a strong influence in guild structure is
52 expected because this information transmission may reduce competition costs [8–11].

53 Carrion is an unpredictable and ephemeral resource that can be exploited by many species, even
54 at the same time [12]. Thus social mechanisms to facilitate carrion location and consumption
55 may be selected among scavenger species, since individual foraging would be very costly
56 [13,14]. Social information can pass through individuals unintentionally as cues, e.g., vultures
57 flying in circles and descending to the ground attract other vultures and carnivores [15–17]; or
58 intentionally as signals to obtain something in return, e.g. corvids attract raptors or mammalian
59 carnivores to carcasses to tear the skin and access the meat, as they do not have the capacity to
60 do so [1,18].

61 Many studies have mentioned the facilitation between scavenger species in locating carrion, but
62 very few have described and analysed this process in detail [15,19,20]. For obligate scavengers
63 (i.e., vultures), it is not exactly known how social transmission occurs when vultures locate
64 carcasses, but there are two hypotheses about it. On the one hand, the “local enhancement”
65 hypothesis, whereby individuals locate carcasses by seeing conspecifics feeding at a point
66 [20,21]. On the other hand, the "vulture chains" hypothesis states that vultures establish visual
67 chains while they are flying to the carcass, that are used for carrion signalling [13]. In either
68 case, there is a positive influence of the number of vultures arriving at a carcass and a decrease
69 in the time needed for the arrival of new individuals [13,21]. So far, these two assumptions have
70 been established and tested intraspecifically for a single vulture species, even if different vulture
71 species can feed together in a carcass at the same time [22–24].

72 As described for other guilds, there may be interspecific differences in the scavenger
73 information transmission cascades [3]. Some species may "initiate" or "lead" the information
74 transmission process, being important for the maintenance of these cascades and thus for the
75 carrion consumption process [25,26]. In particular, it has been suggested that information
76 transmission mechanisms (i.e., capacity to generate and use information provided by others)

77 may be more deeply rooted in specialist (e.g., vultures) than in generalist species (e.g.,
78 facultative species) [2,19]. Also, the generation and use of social information can depend on
79 species competitive ability (e.g., due to differences in size) and foraging efficiency (e.g., use of
80 different senses) [3,27]. Thus, the likelihood of individuals to join, follow or stay feeding at a
81 carcass can depend on the presence of other species with particular traits (e.g., largest beak,
82 ability to smell), translating into characteristic patterns of arrival of the species to the carcass
83 [15]. The analysis of temporal data on species occurrence combined with species traits may
84 indicate what benefits may be sought by some species following others [3,28].

85 Experimental work is still critically needed to determine what social information is used and
86 how it is used in different natural scenarios. Therefore, in this study we aim to combine data
87 obtained through the monitoring of carcasses in the field and the realization of models in which
88 we analyse possible information transmission cascades within a Neotropical scavenger
89 community. This guild has been less studied, even though some vulture species have a
90 developed sense of smell. Therefore, we identify and rank the scavenger species that influence
91 the process of locating and recruitment at carcasses according to different species traits (e.g.,
92 morphological or behavioural attributes) that define their roles within the assemblage [10,11].
93 We tested (1) if scavengers use social information to find carcasses, in particular, if species with
94 higher foraging efficiency (i.e., developed sense of smell) arrive first, discovering carcasses and
95 serving as cues for others, (2) if the information transmission occurs immediately through local
96 enhancement or if the time-scale at which the transmission takes place is longer, (3) how the
97 presence and abundance of species with different competitive capacities influence the
98 information transmission within the assemblage, and thus the order of arrival of species to a
99 carcass, and (4) which species traits are most influential in the generation of information and its
100 social transmission.

101 ## Methods

102 ### Study area and scavenger community

The fieldwork was carried out in the *Cerrado* savanna, Piauí state, North-eastern Brazil. This biome has a tropical climate with two seasons, the dry season (i.e., from April to September) and the wet season (i.e., from October to March). The vegetation is very diverse, ranging from grasslands to closed forest canopy [29,30]. This area holds four species of American vultures (Cathartidae): turkey (*Cathartes aura*), lesser yellow-headed (*Cathartes burrovianus*), American black (*Coragyps atratus*) and king (*Sarcoramphus papa*) vultures. Also, facultative scavengers are present, including five species of other raptors, such as southern caracaras (*Caracara plancus*) and yellow-headed caracaras (*Milvago chimachima*), as well as mammals (5 species), reptiles (3) and other facultative birds (2) (further details in Table S1) [31].

Study design and variables

During November 2018, we placed 55 carcasses differentiated into two sizes: large carcasses (n = 10), between 20 – 40 kg, corresponding to goat carcasses; and small carcasses (n= 45), in which we grouped chicken pieces and whole chickens, between 0.075 – 2 kg. We monitored each carcass until its complete consumption (48.41 ± 14.41 hours for large carcasses and 13.55 ± 19.56 hours for small carcasses) [31] using two automatic cameras (Browning Strike Force pro HD), one set up to take images and the other to take videos (see [31] for more details). The camera was automatically activated by the animal when it was detected. We placed carcasses separating the larger ones by a minimum of 1.5 km and the smaller ones by a minimum of 150 m, considering them as independent replicates (see [31] for more details of the location of the carcasses). Carcasses were placed during the day, both in the morning (before 12:00, n = 31) and in the afternoon (up to sunset, n = 24).We worked mainly with the images, but we used the videos (henceforth both called 'archives') when we did not have any image due to camera failure. We obtained a total of 27,092 archives (i.e., 24,624 for goat carcasses and 2,468 for chicken carcasses). For each one, we determined 1) the carcass to which it belongs (i.e., carcass ID), 2) the date and time when the archive was taken, 3) the time between carcass placement and the archive ('time since carcass placement'), 4) the species present in the archive ('presence'), and 5) their abundances, i.e., the numbers of individuals of each species

130 ('abundance'). We further quantified, for each carcass, the percentage of shrub and tree cover in
131 a 5-meter radius around the point where we placed the carcass ('vegetation cover'). Vegetation
132 cover could affect information transmission, so that a higher cover would make it more difficult
133 for a species to receive visual cues [11,32].

134 **Statistical analysis**

135 Because differences in community structure and consumption patterns were found between the
136 two carcass sizes [31], we analysed the data for large and small carcasses separately. The use of
137 camera-trap data to model multi-species time-series dynamics is complicated because the
138 images are not taken at regular intervals, but only when a species is present. Thus, the absence
139 of a species is indicated by the absence of images from it, but this should be considered as data
140 (on species absence), not as missing data. To resolve this, we converted the irregular camera-
141 trap data into regular interval data. We denoted the time interval by Δt, and used $\Delta t = 10$ min
142 in our main analyses (see Supporting information for sensitivity analyses where we use either
143 Δt =1 minute or $\Delta t = 1$ hour instead). We denoted by y_{ijt} the maximum count of individuals
144 of species j in carcass i from any image taken during time interval t. We indexed time so that
145 $t = 1$ corresponds to the interval starting when the carcass was placed into the field.

146 Our main focus was to ask how the first arrival time of each focal species depends on the
147 previous presence of heterospecifics. We included as 'focal species' those species that had
148 appeared in at least 5 carcasses and used the first occurrence (i.e., first arrival) in each of the
149 carcasses as the response variable (see Table S1). To account for possible confounding effects
150 (not related to species interactions) that we thought could be influencing species arrival, we first
151 established a baseline model in which we modelled 'focal species' abundance y_{ijt} with a
152 Poisson regression, where we used as predictors (i) 'vegetation cover', (ii) 'time of the day', and
153 (iii) 'time since carcass placement'. We included 'vegetation cover' as a continuous covariate
154 ranging from 0 to 1. We included 'time of the day' through linear combination of the periodic
155 functions $\sin(2\pi h/24)$ and $\cos(2\pi h/24)$, where $h \in [0,24]$ is the hour of the day when the
156 image or video was taken. We included both first and second order effects of 'time since carcass

157 placement' to account for the species abundances peaking at intermediate times since carcass
158 placement. We note that the influence of 'time since carcass placement' can be either due to
159 confounding factors (e.g., the stage of decay of the carcass) or due to species interactions (e.g.,
160 the late arrival of the species being explained by the focal species using other species as a cue).
161 As these two cannot be conclusively separated from observational data, we performed a
162 sensitivity analysis where 'time since carcass placement' was either included or excluded in the
163 baseline model (see Supporting information). We denoted the linear predictor of the fitted
164 baseline model by L_{ijt}. We note that this linear predictor summarizes the effects of all
165 confounding effects into a single variable.

166 To ask how the first arrival times of the species depend on the presence of heterospecifics, we
167 followed a survival-modelling strategy. We denoted by p_{ijt} the presence ($p_{ijt} = 1$
168 corresponding to $y_{ijt} > 0$) or absence ($p_{ijt} = 0$ corresponding to $y_{ijt} = 0$) of species j in
169 carcass i from any image taken during time interval t. We considered, for each carcass and each
170 'focal species', the data only until the first arrival of each of the species, so that the sequence of
171 the data p_{ijt} (i.e., response variable) over time intervals t is of the form of a series of zeros
172 (absences) followed by one (presence). We modelled these data with logistic regression, where
173 the predictors (i.e., explanatory variables) were the linear predictor L_{ijt} from the baseline model
174 (to account for confounding effects and avoid overloading the model with covariates due to our
175 small sample size), and the presence of other species in earlier times h_{ijt}. To consider the
176 possibility of a species arriving at the carcass regardless of whether another species has been
177 there previously, we consider the model that only includes the linear predictor L_{ijt} (i.e., without
178 including the previous presence of another species) as a null model. In particular, the first and
179 second order effects of 'time since carcass placement' model the baseline probability of when
180 the focal species typically appears to the carcass. If the prior presence of some other species
181 turns out to have e.g., a positive effect, it means that, the focal species is likely to appear earlier
182 than predicted by the null model if prior presence of other species was recorded in the carcass,

whereas it is likely to appear later than predicted by the null model if prior presence of other species was not recorded in the carcass.

We considered several alternatives to define the presence of other species in earlier times (h_{ijt}) to evaluate different hypotheses for the transmission of information between species. We varied the following axes: (A) who the influencer is (i.e., the species or set of species that arrive in the carcass prior to the focal species and that may be influencing its appearance); (B) at what time-scale the influence takes place (i.e., how long does the visual cue of the presence of other species last); (C) is it the presence or abundance of the influencer that matters? Concerning (A), we either considered (A1) all the species other than the focal species irrespective of their identity; (A2) those avian species that can smell, i.e., *Cathartes* species, with an olfactory bulb up to four times larger than other sympatric vultures (e.g., black vultures) [33–35]; (A3) each individual species, however restricting the analyses to only those species detected occurring before the focal species at least five times. Concerning (B), we considered the data for the influencer either (B1) during the previous 10 minutes; (B2) during the previous 30 minutes; (B3) during the previous hour, following the methodology established by Orr et al. (2019); or (B4) during the previous 4 hours; to detect whether information cascades were occurring on a larger time scale, as would occur in the vulture chain hypothesis. Concerning (C), we considered (C1) the presence-absence of the influencer, (C2) the proportion of time-intervals during which the influencer was present; or (C3) the maximum abundance of the influencer during the focal time period (i.e., values determined in the alternatives of hypothesis B). Some of these predictors are correlated, and thus they are not independent alternatives, but comparison about their relative fits to the data may, however, yield valuable suggestions on the likely drivers of the heterospecific interactions.

All analyses were conducted in the R programming environment [36] using generalized linear models (GLMs) with a Poisson distribution (log link function) or a Bernoulli distribution (logit link function). For GLMs we used the *glm* function in the *lme4* package [37]. We selected the best models based on Akaike's information criteria for small samples (AICc) from all potential

models (including null model) using the *AICc* function in the *MuMIn* package [38], and we choose only those with an ΔAICc <2 (i.e., top-ranking models) [39]. Finally, we calculated the goodness of fit for the top-ranking models through the percentage of deviance explained (D^2) [39]:

$$D^2 = \frac{null\ deviance - residual\ deviance}{null\ deviance}\ x\ 100$$

Results

Some species in the community were recorded commonly as the first to reach the carcass (e.g., *Cathartes* species, with a first arrival time of 25.61 ± 17.82 hours), while we never observed some other species to arrive as the first ones (Fig. 1). The arrival of the species to large carcasses was more predictable than their arrival to small carcasses, as for small carcasses there was a greater variability in the times it took for species to reach the carcass (Fig. 1, see Table S2 for further details).

We observed a several cases where species influenced each other's arrival positively, but not any case of a negative influence (Fig. 2). In particular, the king vulture and the southern caracara were positively influenced by the previous occurrences of the other species. This result was highly robust, as we observed such a positive influence almost independently on how we constructed the biotic predictor, i.e., whether we considered as the influencer all species or only some of them, whether we considered the *presence* or *abundance* of the influencer, or whether we considered the *presence* of the influencer over short or long time-intervals (the predominance of green squares in Fig. 2 for these species). Furthermore, these results held whether we discretized the data to Δt=1 min, Δt=10 min or Δt=1 hour interval, and whether we included or excluded the *time since carcass placement* in the baseline model (see Supporting Information). Interestingly, for both the king vulture and the southern caracara, at large carcasses we observed the strongest influence of the *abundances* of *all other species*, whereas at small carcasses the *presence* of influencers *with olfaction* (especially the turkey vulture; with a first arrival time to small carcasses of 29.14 ± 17.00 hours, Table S2) had the highest effect,

being included in the top-ranking models (green squares marked with thick borders in Fig. 2). Also at small carcasses, the lesser yellow-headed vulture (19.60 ± 18.43 hours, Table S2) was influenced by the previous *presence* of *all other species*, especially by the proportion of time that the other species were present shortly before the focal time (i.e., alternatives of B; Fig. 2).

Our results were not conclusive on whether the American black vulture was or was not influenced by the previous *presence* of heterospecifics, as in some of the model variants we did record a significant effect while in other model variants we did not do so (see Supporting Information). We did not obtain any influence of heterospecifics on their arrival for turkey vultures, hoary foxes (19.13 ± 10.46 hours) and the black-and-white tegu (31.45 ± 18.51 hours), either because there were not enough previous occurrences of other species to fit the models, or because their influences were not significant (Fig. 2). As expected, the linear baseline predictor L_{ijt} had a positive effect for all species, even if the effect was not significant for some cases (Fig. 2).

Discussion

Disentangling the use of social information between species that share a resource and exhibit different foraging capabilities is fundamental to understand the interspecific interactions and how a guild is structured [40]. Our results show how the use of different senses (smell and vision) to find carrion allows for facilitation processes through the transmission of information between scavengers in a Brazilian *cerrado* community. American vulture species with high olfactory ability are the first to arrive at the carcasses and initiate visual information cascades that will indicate species with a lower foraging efficiency (e.g., limited olfactory ability) the presence of the carcasses. In general, signal reception and subsequent response seem to take place in short times, which supports the "local enhancement" hypothesis, so that when any individual sees a heterospecific feeding at a location, it may approach and locate the carcass [13,41]. Furthermore, these patterns of information transmission appear to be strongly influenced by the size of the resource, being fundamental in the location of small carcasses.

Our findings support that scavenger species in this Neotropical guild rely on olfactory (e.g., *Cathartes* vultures, mammals) and visual cues (e.g., most avian scavengers) to locate carcasses. This result contrasts with the foraging behaviour of scavenger guilds in Eurasia and Africa, in which only mammals have a highly developed sense of smell, whereas vultures rely only on visual cues to locate carrion [35,42]. In our system, vulture species with a developed sense of smell seem to have a clear advantage over those lacking this ability, since they are the first ones that arrive to most carcasses [24,43]. This dominance of vultures at large and small carcasses in Neotropical ecosystems contrasts with the dominant role of meso-carnivores and raptors at small carcasses in other biomes [44].

We highlight the role of the turkey vulture, as it is consistently the first one locating large carcasses and it does not depend on any species to locate the smaller ones [24,35,45]. On the contrary, our models show that the first occurrence of the lesser yellow-headed vulture depends on the previous presence of other species, despite they had short arrival times and a highly developed sense of smell [34,42,46]. Therefore, our findings could be due to differences in these species' relative abundance in the study area (authors, unpublished data).

Foraging behaviour refers to both the acquisition of resources and the way in which information about those resources is acquired (i.e., personal experience and social information) [47]. Although our data are correlational, our results show the existence of temporal associations between species, suggesting a facilitation process locating carrion (i.e., increase in foraging efficiency), since the presence of heterospecifics at the carcasses positively influences the appearance of new species [5,48]. This agrees with social information taking a fundamental role when resources are unpredictable, as happens with carrion [49]. Previous research has shown that species using different foraging behaviour (e.g., different senses) act as initiators of mixed-species feeding aggregations in multiple systems [50,51]. Our results show that vulture species with developed sense of smell generate this information, since their presence serves as a visual cue for other species to locate the carcasses. Our findings also show that, once a species with olfactory capacity arrives at the carcass, the rest of the species may join independently of the

identity of the species, creating information cascades but without following a specific order of arrival. Through the reception of social information, individuals with lower foraging capacity may visually follow the ones with higher capacity (e.g., developed olfaction) that have previously arrived to the carrion following olfactory cues [18]. However, the decision to join a group of individuals from other species must involve a balance between the potential benefits (e.g., access to the resource) and costs (e.g., aggressive interactions) [2]. Similarly, the individual who generates the initial cue (e.g., turkey vultures) will benefit from arriving in first place but is not expected to profit from the arrival of other species, since there is a possibility of being displaced by new individuals who arrive at the carcass (e.g., larger species like king vultures). This has been seen for turkey vultures, which used to be displaced after the arrival of other species [24,27,45].

Furthermore, facilitation processes through social information cascades seem to be influenced by carcass size and the temporal scale. On the one hand, our results show how the presence of species with a developed olfactory capacity (i.e., turkey and yellow-headed vultures) especially influences the arrival of other species at small carcasses. This may be because small carcasses are more difficult to locate, i.e., the intensity of the visual cue is stronger at large carcasses due to their larger size. Although it is also possible that the olfactory cue may be stronger at large carcasses (i.e., more rotting biomass). Therefore, having a developed sense of smell may be a fundamental advantage for reaching small carcasses first, since the difficulty of finding them is higher. In addition, at small carcasses the mere presence of an individual from another species would serve as a visual signal, while at large carcasses the maximum abundance is more important. This could be because the number of individuals consuming a carcass is larger at the large ones, generating a stronger visual signal [31]. On the other hand, cues were perceived on a different time scale by the different species, since some of them arrived at the carcass immediately upon perception of the cue (e.g., 10 minutes) and others required longer periods of time (e.g., up to 4 hours). This could be because not all species respond to the presence of other species equally, probably due to differences in foraging efficiency, abundance and competitive

316 abilities among them [52,53]. We found that most species responded quickly to the previous
317 presence of heterospecifics, which supports the "local enhancement" hypothesis against the
318 hypothesis of a wider chain of information (e.g., "vulture chains" hypothesis) [41].

319 Interestingly, mammals and reptiles do not seem to be influenced by the previous presence of
320 other species. This contradicts what happens in other systems where birds influence the arrival
321 (i.e., recruitment) of carnivores, or vice versa [15,17]. Both mammals and reptiles have a
322 developed sense of smell and chemoreception, respectively, which would allow them to locate
323 carrion without depending on vulture species. This lack of use of social information may be also
324 due to the quick consumption of small carcasses (i.e., the only ones that are consumed by most
325 facultative scavengers), as the first individual to locate the carcass is the one consuming it
326 completely in most cases [31].

327 Our study highlights how the use of different senses (i.e., smell and sight) within a Neotropical
328 scavenger guild gives rise to facilitation processes in locating carcasses using heterospecific
329 social information. Species with a higher efficiency in finding carcasses (e.g., highly developed
330 smell) play a key role in this process, as they seem to serve as visual cue for the rest of the
331 species. The use and transmission of social information is subject to strong selection pressures
332 and can influence since the individuals from the same or different species to the community
333 structure [9,10]. This makes essential to continue investigating how senses influence the
334 processes of social information transmission and its relative importance depending on different
335 factors, considering both heterospecific and conspecific information, and including all the
336 species of the scavenging community.

337 **Acknowledgements**

338 LNA, ZMR, and ESG were supported by the Generalitat Valenciana and the European
339 Social Fund (ACIF/2019/056, APOSTD/2019/016, SEJI/2018/024, respectively). ZMR
340 was also funded by the Junta de Andalucía (POSTDOC_21_00353). ESG also received
341 the grant RYC2019-027216-I funded by MCIN/AEI/ 10.13039/501100011033 and by ESF

342 Investing in your future. OO was funded by Academy of Finland (grant no. 309581), Jane
343 and Aatos Erkko Foundation, Research Council of Norway through its Centres of
344 Excellence Funding Scheme (223257), and the European Research Council (ERC)
345 under the European Union's Horizon 2020 research and innovation programme (grant
346 agreement No 856506; ERC-synergy project LIFEPLAN).

347 **Data accessibility**

348 All the raw data and analysis code used during the current study are available in the Figshare
349 Digital Repository [54]

350 **References**

351 1. Danchin É, Giraldeau LA, Valone TJ, Wagner RH. 2004 Public information: From nosy
352 neighbors to cultural evolution. *Science (80-.).* **305**, 487–491.
353 (doi:10.1126/science.1098254)

354 2. Martínez AE, Pollock HS, Kelley JP, Tarwater CE. 2018 Social information cascades
355 influence the formation of mixed-species foraging aggregations of ant-following birds in
356 the Neotropics. *Anim. Behav.* **135**, 25–35. (doi:10.1016/j.anbehav.2017.10.024)

357 3. Goodale E *et al.* 2020 Mixed company: a framework for understanding the composition
358 and organization of mixed-species animal groups. *Biol. Rev.* **95**, 889–910.
359 (doi:10.1111/brv.12591)

360 4. Langrock R *et al.* 2014 Modelling group dynamic animal movement. *Methods Ecol.*
361 *Evol.* **5**, 190–199. (doi:10.1111/2041-210X.12155)

362 5. Galef BG, Giraldeau L-AA. 2001 Social influences on foraging in vertebrates: causal
363 mechanisms and adaptive functions. *Anim. Behav.* **61**, 3–15.
364 (doi:10.1006/anbe.2000.1557)

365 6. Giraldeau LA, Valone TJ, Templeton JJ. 2002 Potential disadvantages of using socially

366 acquired information. *Philos. Trans. R. Soc. B Biol. Sci.* **357**, 1559–1566.
367 (doi:10.1098/rstb.2002.1065)

368 7. Laland KN. 2004 Social learning strategies. **32**, 4–14.

369 8. Jaakkonen T, Kivelä SM, Meier CM, Forsman JT. 2015 The use and relative importance
370 of intraspecific and interspecific social information in a bird community. *Behav. Ecol.*
371 **26**, 55–64. (doi:10.1093/beheco/aru144)

372 9. Seppänen JT. 2007 Social information use is a process across time, space, and ecology,
373 reaching heterospecifics (Ecology (2007) 88 (1622-1633)). *Ecology*. **88**, 2950.
374 (doi:10.1890/0012-9658(2007)88[2950:E]2.0.CO;2)

375 10. Goodale E, Beauchamp G, Magrath RD, Nieh JC, Ruxton GD. 2010 Interspecific
376 information transfer influences animal community structure. *Trends Ecol. Evol.* **25**, 354–
377 361. (doi:10.1016/j.tree.2010.01.002)

378 11. Orr MR, Nelson JD, Watson JW. 2019 Heterospecific information supports a foraging
379 mutualism between corvids and raptors. *Anim. Behav.* **153**, 105–113.
380 (doi:10.1016/j.anbehav.2019.05.007)

381 12. DeVault TL, Rhodes Olin E J, Shivik JA, Rhodes OE, Shivik JA. 2003 Scavenging by
382 vertebrates: behavioral, ecological, and evolutionary perspectives on an important energy
383 transfer pathway in terrestrial ecosystems. *Oikos* **102**, 225–234. (doi:10.1034/j.1600-
384 0706.2003.12378.x)

385 13. Jackson AL, Ruxton GD, Houston DC. 2008 The effect of social facilitation on foraging
386 success in vultures: A modelling study. *Biol. Lett.* **4**, 311–313.
387 (doi:10.1098/rsbl.2008.0038)

388 14. Ruxton GD, Houston DC. 2004 Obligate vertebrate scavengers must be large soaring
389 fliers. *J. Theor. Biol.* **228**, 431–436. (doi:10.1016/j.jtbi.2004.02.005)

390 15. Kane A, Kendall CJ. 2017 Understanding how mammalian scavengers use information

391 from avian scavengers: cue from above. *J. Anim. Ecol.* **86**, 837–846. (doi:10.1111/1365-
392 2656.12663)

393 16. Veen J. 1977 Functional and Causal Aspects of Nest Distribution in Colonies of the
394 Sandwich Tern (Sterna s. sandvicencis Lath.). *Behaviour* **Suppl. XX**, 1–193.

395 17. Kruuk H. 1967 Competition for food between vultures in East Africa. *Ardea* **55**, 171.

396 18. Heinrich B. 1988 Winter foraging at carcasses by three sympatric corvids, with emphasis
397 on recruitment by the raven, Corvus corax. *Behav. Ecol. Sociobiol.* **23**, 141–156.
398 (doi:10.1007/BF00300349)

399 19. Jackson CR *et al.* 2020 A dead giveaway: Foraging vultures and other avian scavengers
400 respond to auditory cues. *Ecol. Evol.* , 1–6. (doi:10.1002/ece3.6366)

401 20. Kane A, Jackson AL, Ogada DL, Monadjem A, McNally L. 2014 Vultures acquire
402 information on carcass location from scavenging eagles. *Proc. R. Soc. B Biol. Sci.* **281**,
403 20141072. (doi:10.1098/rspb.2014.1072)

404 21. Cortés-Avizanda A, Jovani R, Donázar JA, Grimm V. 2014 Bird sky networks: How do
405 avian scavengers use social information to find carrion? *Ecology* **95**, 1799–1808.
406 (doi:10.1890/13-0574.1)

407 22. Kendall C, Virani MZ, Kirui P, Thomsett S, Githiru M. 2012 Mechanisms of coexistence
408 in vultures: Understanding the patterns of vulture abundance at carcasses in Masai Mara
409 National Reserve, Kenya. *Condor* **114**, 523–531. (doi:10.1525/cond.2012.100196)

410 23. Moreno-Opo R, Trujillano A, Margalida A. 2020 Larger size and older age confer
411 competitive advantage: dominance hierarchy within European vulture guild. *Sci. Rep.*
412 **10**, 1–12. (doi:10.1038/s41598-020-59387-4)

413 24. Houston DC. 1988 Competition for food between Neotropical vultures in forest. *Ibis*
414 *(Lond. 1859).* **130**, 402–417. (doi:10.1111/j.1474-919X.1988.tb08815.x)

415 25. Hoffman W, Heinemann D, Wiens JA. 1981 The ecology of seabird feeding flocks in

Alaska. *Auk* , 437–456.

26. Harrison NM, Whitehouse MJ. 2011 Mixed-species flocks: An example of niche construction? *Anim. Behav.* **81**, 675–682. (doi:10.1016/j.anbehav.2011.01.013)

27. Buckley NJ. 1997 Experimental tests of the information-center hypothesis with black vultures (Coragyps atratus) and turkey vultures (Cathartes aura). *Behav. Ecol. Sociobiol.* **41**, 267–279. (doi:10.1007/s002650050388)

28. Sridhar H, Shanker K. 2013 Using intra-flock association patterns to understand why birds participate in mixed-species foraging flocks in terrestrial habitats. *Behav. Ecol. Sociobiol.* **68**, 185–196. (doi:10.1007/s00265-013-1633-3)

29. Ratter JA, Ribeiro JF, Bridgewater S. 1997 The Brazilian cerrado vegetation and threats to its biodiversity. *Ann. Bot.* **80**, 223–230. (doi:10.1006/anbo.1997.0469)

30. Ribeiro JF, Walter BMT. 1998 Fitofisionomias do bioma Cerrado. In *Cerrado: ambiente e flora*, pp. 87-166.

31. Naves-Alegre L, Morales-Reyes Z, Sánchez-Zapata JA, Durá-Alemañ CJ, Gonçalves Lima L, Machado Lima L, Sebastián-González E. 2021 Uncovering the vertebrate scavenger guild composition and functioning in the Cerrado biodiversity hotspot. *Biotropica* **53**, 1582–1593. (doi:10.1111/btp.13006)

32. Pardo-Barquín E, Mateo-Tomás P, Olea PP. 2019 Habitat characteristics from local to landscape scales combine to shape vertebrate scavenging communities. *Basic Appl. Ecol.* **34**, 126–139. (doi:10.1016/j.baae.2018.08.005)

33. Potier S. 2019 Olfaction in raptors. *Zool. J. Linn. Soc.* , 1–10. (doi:10.1093/zoolinnean/zlz121)

34. Grigg NP, Krilow JM, Gutierrez-Ibanez C, Wylie DR, Graves GR, Iwaniuk AN. 2017 Anatomical evidence for scent guided foraging in the Turkey vulture. *Sci. Rep.* **7**, 1–10. (doi:10.1038/s41598-017-17794-0)

441 35. Potier S, Duriez O, Célérier A, Liegeois JL, Bonadonna F. 2019 Sight or smell: which
442 senses do scavenging raptors use to find food? *Anim. Cogn.* **22**, 49–59.
443 (doi:10.1007/s10071-018-1220-0)

444 36. R Core Team. 2013 R: A language and environment for statistical computing.

445 37. Bates D, Sarkar D, Bates MD, Matrix L. 2007 The lme4 package. *R Packag. version* **2**,
446 74.

447 38. Bartoń K. 2019 Package 'MuMIn': Multi-model inference. *R Packag. ver. 1.43. 6* ,
448 <https://cran.r-project.org/web/packages/MuMIn>.

449 39. Burnham KP, Anderson DR. 2002 *Model selection and multimodel inference. A*
450 *practical information-theoretic approach*. Springter.

451 40. Forsman JT, Seppänen JT, Mönkkönen M. 2002 Positive fitness consequences of
452 interspecific interaction with a potential competitor. *Proc. R. Soc. B Biol. Sci.* **269**,
453 1619–1623. (doi:10.1098/rspb.2002.2065)

454 41. Arbilly M, Laland KN. 2014 The local enhancement conundrum: In search of the
455 adaptive value of a social learning mechanism. *Theor. Popul. Biol.* **91**, 50–57.
456 (doi:10.1016/j.tpb.2013.09.006)

457 42. Houston DC. 1985 Evolutionary Ecology of Afrotropical and Neotropical Vultures in
458 Forests. *Ornithol. Monogr.* **36**, 856–864. (doi:10.2307/40168321)

459 43. Houston DC. 1986 Scavenging Efficiency of Turkey Vultures in Tropical Forest. *Condor*
460 **88**, 318–323. (doi:10.2307/1368878)

461 44. Moleón M, Sánchez-Zapata JA, Sebastián-González E, Owen-Smith N. 2015 Carcass
462 size shapes the structure and functioning of an African scavenging assemblage. *Oikos*
463 **124**, 1391–1403. (doi:10.1111/oik.02222)

464 45. Wallace MP, Temple SA. 1987 Competitive interactions within and between species in a
465 guild of avian scavengers. *Auk* **104**, 290–295.

46. Campbell MON. 2021 Vulture foraging and the chemistry of putrefaction. *Crit. Res. Tech. Anim. Habitat Ecol. Int. Examples* , 153–172.

47. Clark CW, Mangel M. 1984 Foraging and flocking strategies: information in an uncertain environment. *Am. Nat.* **123**, 626–641. (doi:10.1086/284228)

48. Galef BG. 2016 Social Learning in Animals : The Roots of Culture.

49. Deygout C, Gault A, Duriez O, Sarrazin F, Bessa-Gomes C. 2010 Impact of food predictability on social facilitation by foraging scavengers. *Behav. Ecol.* **21**, 1131–1139. (doi:10.1093/beheco/arq120)

50. Harrison N, Whitehouse M, Heinemann D, Prince P, Hunt G, Veit R. 1991 Observations of Multispecies Seabird Flocks Around South Georgia. *Auk* **108**, 801–810. (doi:10.1093/auk/108.4.801)

51. Duffy DC. 1989 Seabird foraging aggregations: a comparison of two southern upwellings. *Colon. Waterbirds* , 164–175.

52. Kendall CJ. 2013 Alternative strategies in avian scavengers: How subordinate species foil the despotic distribution. *Behav. Ecol. Sociobiol.* **67**, 383–393. (doi:10.1007/s00265-012-1458-5)

53. Reichert MS. 2021 Integrative and Comparative Biology New Dimensions for Animal Communication Networks : Space and Time. , 1–11. (doi:10.1093/icb/icab013)

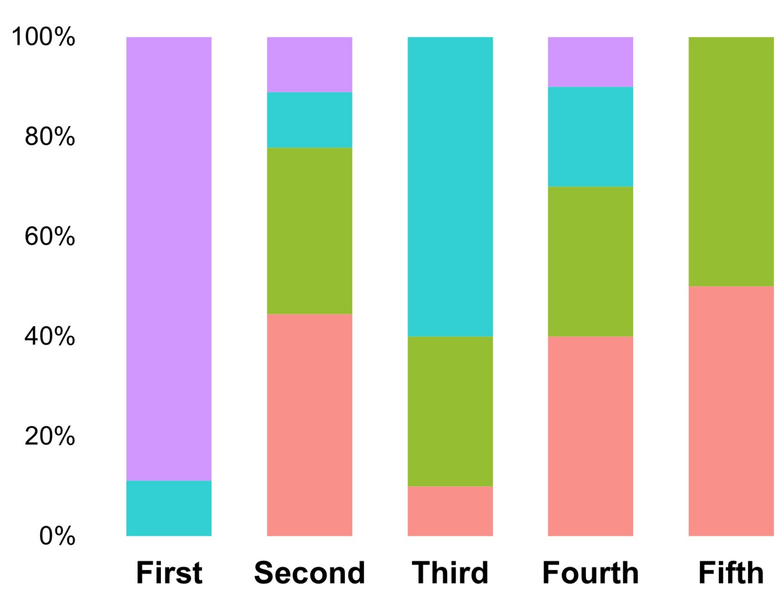
54. Naves-Alegre L, Morales-Reyes Z, Sanchez-Zapata JA, Sebastián-González E, Ovaskainen O. 2022 Data and code from: Scavenging in the realm of senses: smell and vision drive recruitment at carcasses in Neotropical ecosystems. *Figshare* (doi:10.6084/m9.figshare.19665828.v3)

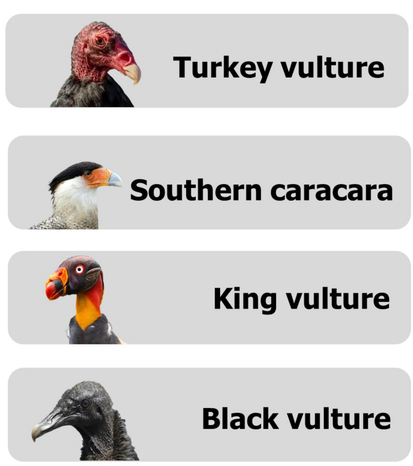
Figure legends

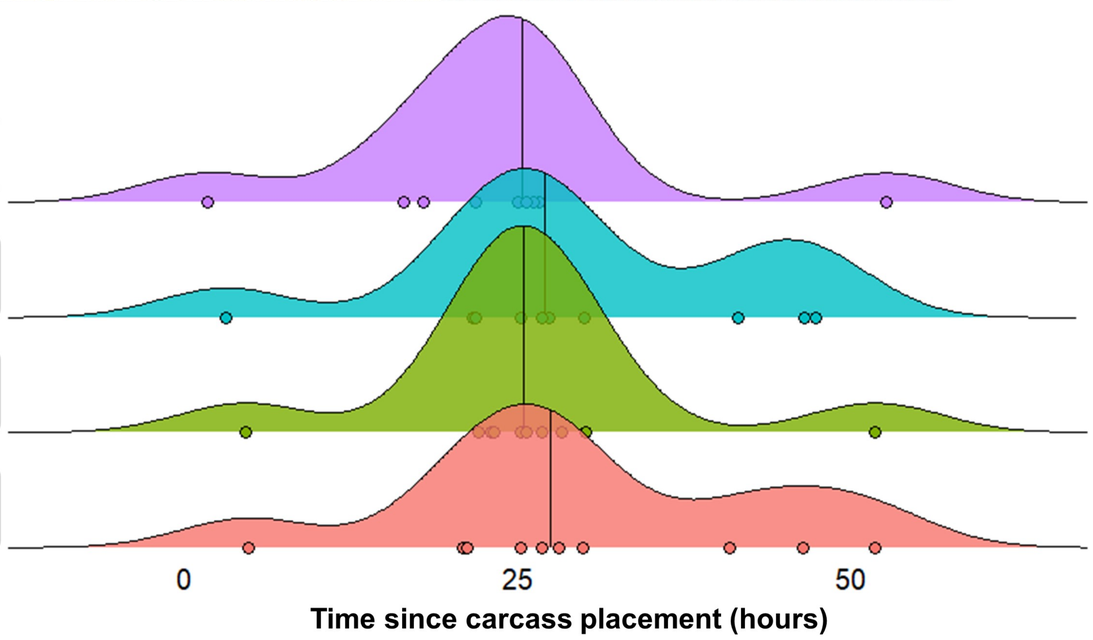
Figure 1. The succession of arrival (bar plots) and arrival time since carcass placement (smoothed plot) of different species to large carcasses and small carcasses. The photographs exemplify consumption patterns, numbers in each image refer to the chronological arrival of a new species and the colour of the number refers to the species. Bar plots represent the percentage of times that each of the focal species (i.e., different colours) reached the carcasses in the different positions (i.e., x-axis; from the first position to the fifth one). The smoothed plots show, for each of the focal species (i.e., y-axis), their frequency with which they arrived at different times since carcass placement (i.e., x-axis in hours). The vertical line in the frequency curves represents the median value of the arrival time for each species. See Table S2 for further details.

Figure 2. Results of the logistic regression on heterospecific influence on first arrival times, shown separately for large and small carcasses. Circles refer to the influence of the baseline predictor L_{ijt}, and the squares to the heterospecific influence. Positive and significant ($p<0.05$) influence on the occurrence (i.e., first appearance) of each focal species is indicated in green; non-significant effects are indicated in grey and model combinations not considered are shown in white. The absence of squares indicates that there is no model for that focal species. The different combinations for B1-B4 (i.e., importance of the presence or abundance of the influencer) and C1-C3 (i.e., previous time considered) assumptions are represented in the mini-squares. See Tables S3 and S4 for further details. The results are shown here for the data discretized to time resolution of Δt=10 min, and for the case where the time since carcass placement was included in the baseline model. See Supporting Information for corresponding results for data discretized to time resolution of Δt=1 min or Δt=1 hour, and the case where the time since carcass placement was excluded in the baseline model.

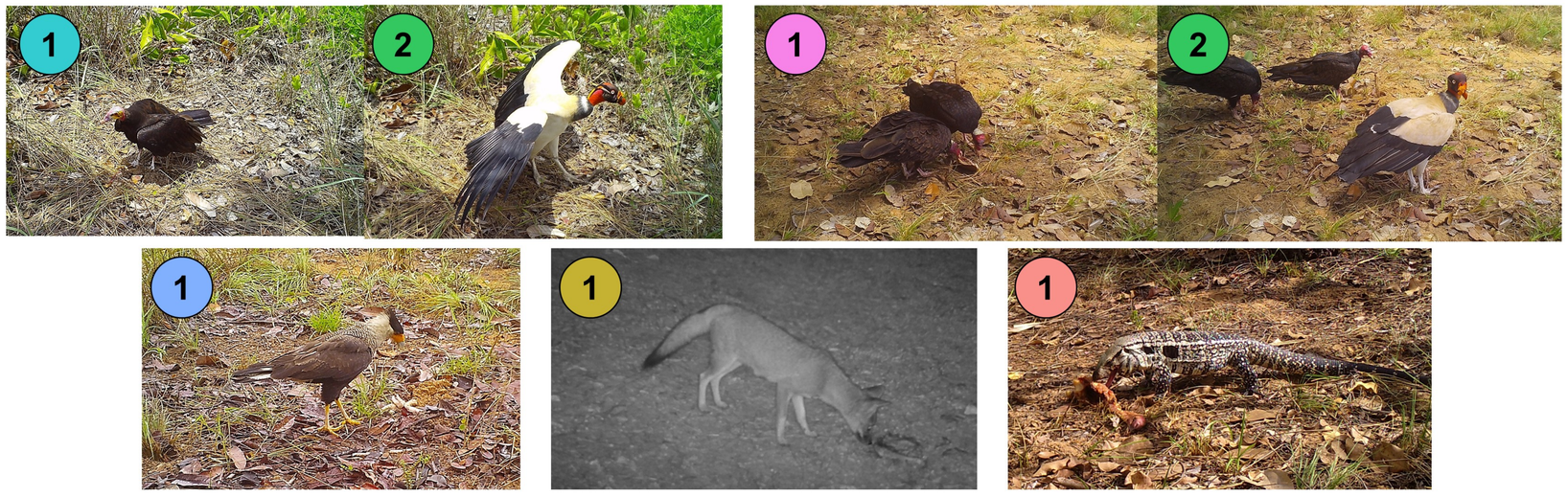
LARGE CARCASSES

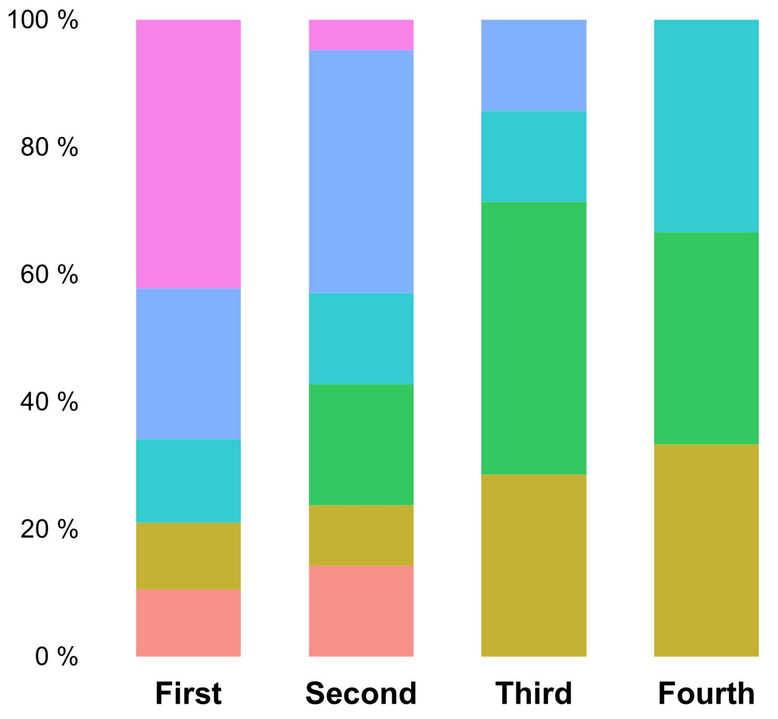


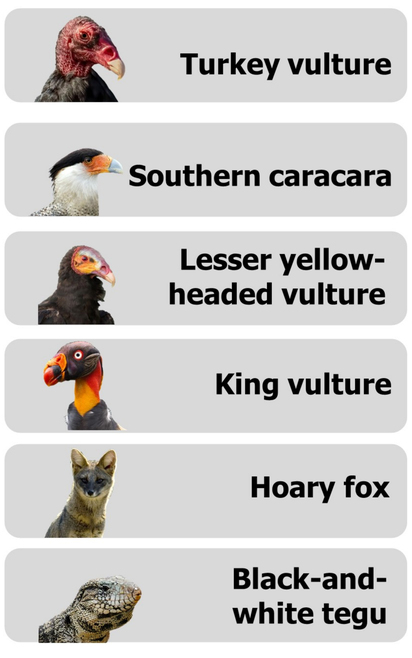


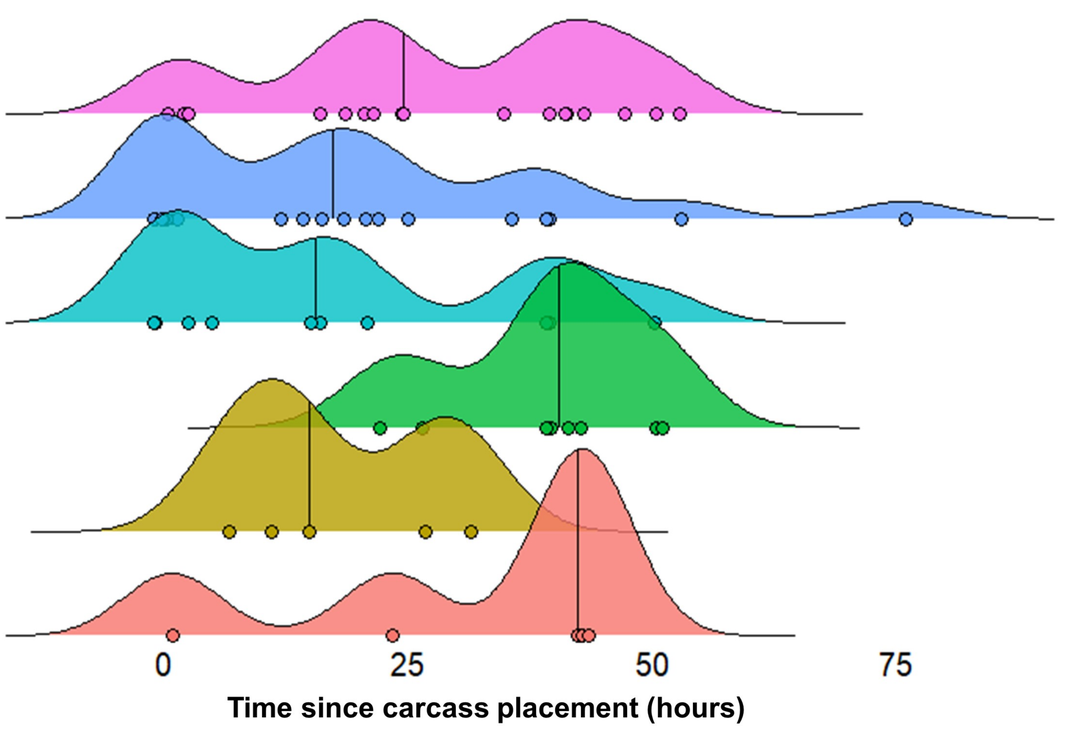


SMALL CARCASSES









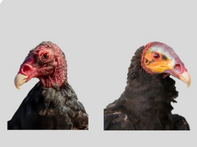
INFLUENCERS

Baseline predictor L_{ijt}

All species

Baseline predictor L_{ijt}

All species



With olfaction

Turkey vulture

FOCAL SPECIES

Turkey vulture

Lesser yellow-headed vulture

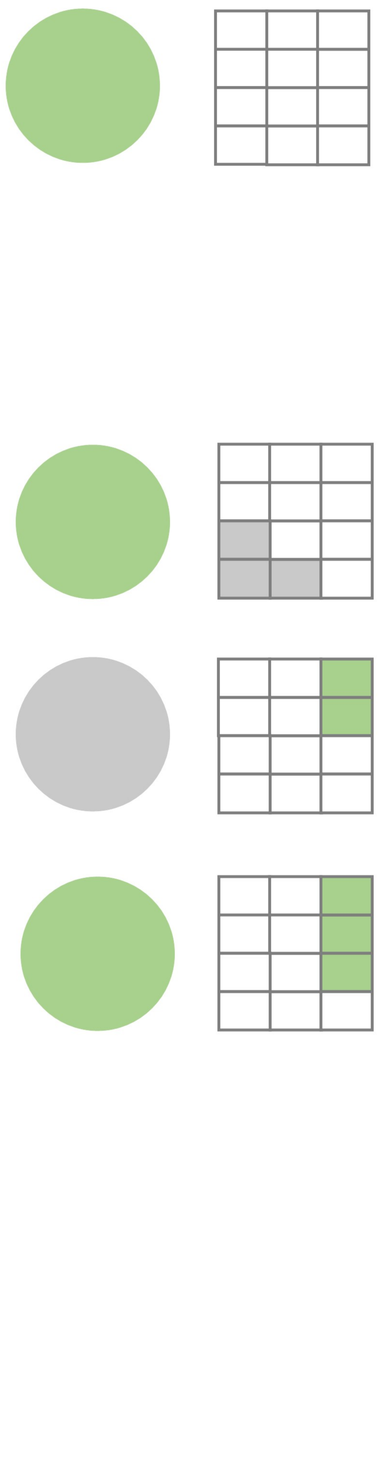
Black vulture

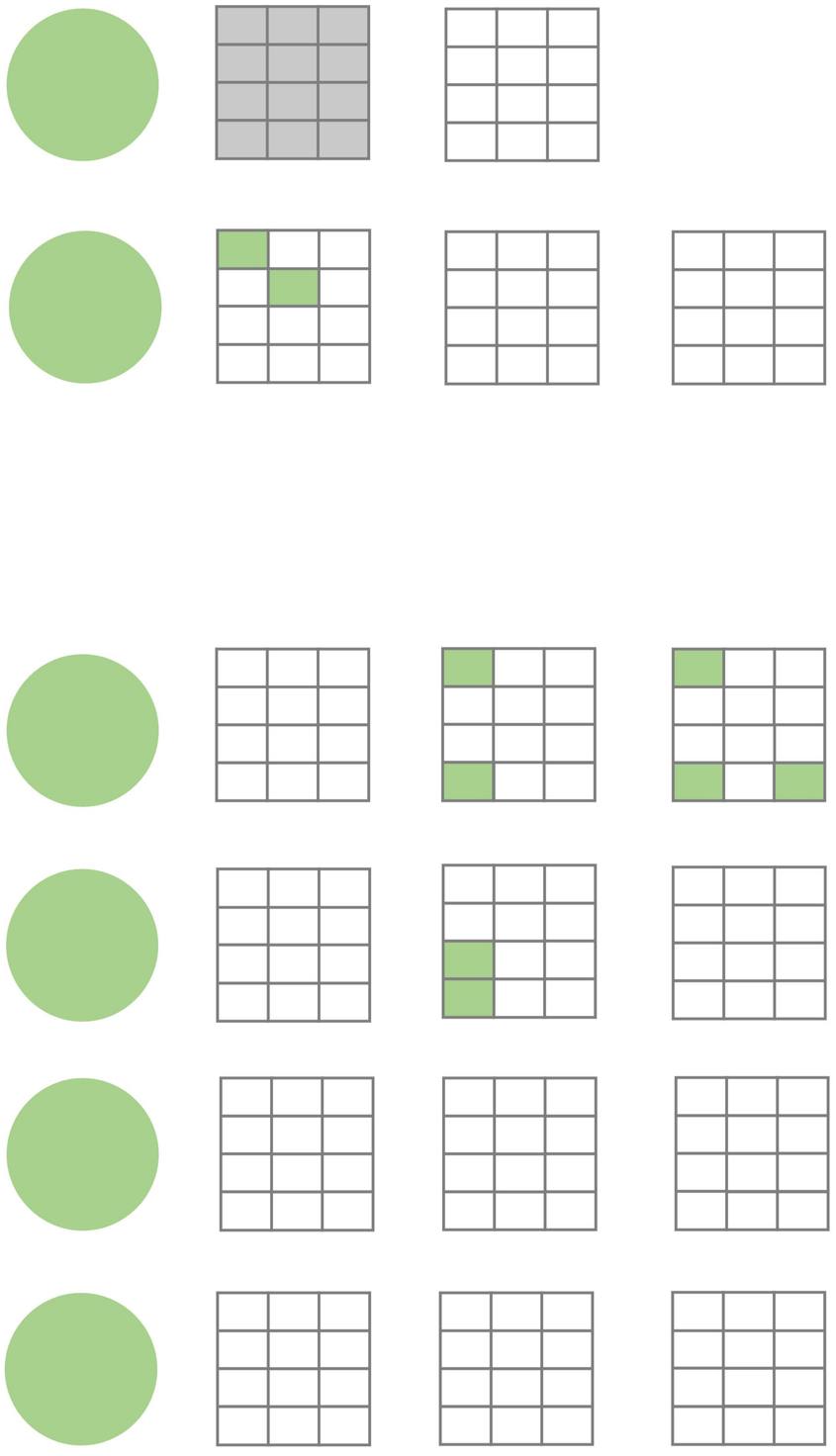
King vulture

Southern caracara

Hoary fox

Black-and-white tegu





Large carcasses

Small carcasses

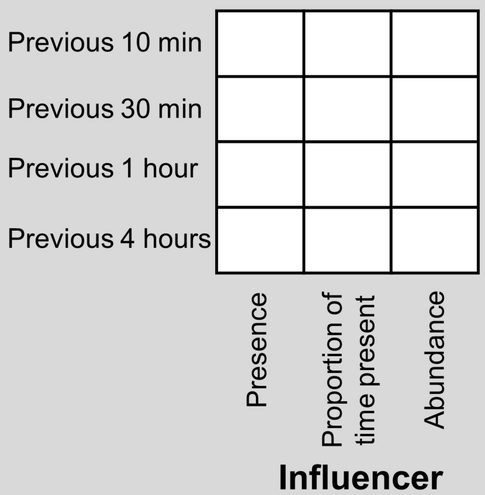
Significant positive effect

Significant negative effect

Not significant effect

Not included

Time-scale of the influence



Influencer