

Research



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

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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.

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

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

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

As described for other guilds, there may be interspecific differences in the scavenger information transmission cascades [3]. Some species may ‘initiate’ or ‘lead’ the information transmission process, being important for the maintenance of these cascades and thus for the carrion consumption process [25,26]. In particular, it has been suggested that information transmission mechanisms (i.e. capacity to generate and use information provided by others) may be more deeply rooted in specialist (e.g. vultures) than in generalist species (e.g. facultative species) [2,19]. Also, the generation and use of social information can depend on species competitive ability (e.g. due to differences in size) and foraging efficiency (e.g. use of different senses) [3,27]. Thus, the likelihood of individuals to join, follow or stay feeding at a carcass can depend on the presence of other species with particular traits (e.g. largest beak, ability to smell), translating into characteristic patterns of arrival of the species to the carcass [15]. The analysis of temporal data on species occurrence combined with species traits may indicate what benefits may be sought by some species following others [3,28].

Experimental work is still critically needed to determine what social information is used and how it is used in different natural scenarios. Therefore, in this study, we aim to combine data obtained through the monitoring of carcasses in the field and the realization of models in which we analyse possible information transmission cascades within a Neotropical scavenger community. This guild has been less studied, even though some vulture species have a developed sense of smell. Therefore, we identify and rank the scavenger species that influence the process of locating and recruitment at carcasses according to different species traits (e.g. morphological or behavioural attributes) that define their roles within the assemblage [10,11]. We tested: (1) if scavengers use social information to find carcasses, in particular, if species with

higher foraging efficiency (i.e. developed sense of smell) arrive first, discovering carcasses and serving as cues for others, (2) if the information transmission occurs immediately through local enhancement or if the timescale at which the transmission takes place is longer, (3) how the presence and abundance of species with different competitive capacities influence the information transmission within the assemblage, and thus the order of arrival of species to a carcass and (4) which species traits are most influential in the generation of information and its social transmission.

2. Methods

(a) Study area and scavenger community

The fieldwork was carried out in the *Cerrado* savannah, Piauí state, Northeastern 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 electronic supplementary material, table S1) [31].

(b) Study design and variables

During November 2018, we placed 55 carcasses differentiated into two sizes: large carcasses ($n = 10$), between 20 and 40 kg, corresponding to goat carcasses; and small carcasses ($n = 45$), in which we grouped chicken pieces and whole chickens, between 0.075 and 2 kg. We monitored each carcass until its complete consumption (48.41 ± 14.41 h for large carcasses and 13.55 ± 19.56 h 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 2468 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 (abundance). We further quantified, for each carcass, the percentage of shrub and tree cover in a 5 m radius around the point where we placed the carcass (vegetation cover). Vegetation cover could affect information transmission so that a higher cover would make it more difficult for a species to receive visual cues [11,32].

(c) Statistical analysis

Because differences in community structure and consumption patterns were found between the two carcass sizes [31], we

analysed the data for large and small carcasses separately. The use of camera-trap data to model multi-species time-series dynamics is complicated because the images are not taken at regular intervals, but only when a species is present. Thus, the absence of a species is indicated by the absence of images from it, but this should be considered as data (on species absence), not as missing data. To resolve this, we converted the irregular camera-trap data into regular interval data. We denoted the time interval by Δt , and used $\Delta t = 10$ min in our main analyses (see electronic supplementary material, information for sensitivity analyses where we use either $\Delta t = 1$ min or $\Delta t = 1$ h instead). We denoted by y_{ijt} the maximum count of individuals of species j in carcass i from any image taken during time interval t . We indexed time so that $t = 1$ corresponds to the interval starting when the carcass was placed into the field.

Our main focus was to ask how the first arrival time of each focal species depends on the previous presence of heterospecifics. We included as ‘focal species’ those species that had appeared in at least five carcasses and used the first occurrence (i.e. first arrival) in each of the carcasses as the response variable (see electronic supplementary material, table S1). To account for possible confounding effects (not related to species interactions) that we thought could be influencing species arrival, we first established a baseline model in which we modelled ‘focal species’ abundance y_{ijt} with a Poisson regression, where we used as predictors: (1) ‘vegetation cover’, (2) ‘time of the day’ and (3) ‘time since carcass placement’. We included ‘vegetation cover’ as a continuous covariate ranging from 0 to 1. We included ‘time of the day’ through linear combination of the periodic 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 image or video was taken. We included both first- and second-order effects of ‘time since carcass placement’ to account for the species abundances peaking at intermediate times since carcass placement. We note that the influence of ‘time since carcass placement’ can be either due to confounding factors (e.g. the stage of decay of the carcass) or due to species interactions (e.g. the late arrival of the species being explained by the focal species using other species as a cue). As these two cannot be conclusively separated from observational data, we performed a sensitivity analysis where ‘time since carcass placement’ was either included or excluded in the baseline model (see electronic supplementary material). We denoted the linear predictor of the fitted baseline model by L_{ijt} . We note that this linear predictor summarizes the effects of all confounding effects into a single variable.

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

species is likely to appear earlier 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 to the carcass prior to the focal species and that may be influencing its appearance); (B) at what timescale 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 min; (B2) during the previous 30 min; (B3) during the previous hour, following the methodology established by Orr *et al.* [11] or (B4) during the previous 4 h; to detect whether information cascades were occurring on a larger timescale, 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 chose only those with an $\Delta AICc$ less than 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]:

$$D^2 = \frac{\text{null deviance} - \text{residual deviance}}{\text{null deviance}} \times 100.$$

3. 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 h), while we never observed some other species to arrive as the first ones (figure 1). The arrival of the species to large carcasses was more predictable than their arrival to small carcasses, as for small carcasses there was greater variability in the times it took for species to reach the carcass (figure 1, see electronic supplementary material, table S2 for further details).

We observed several cases where species influenced each other’s arrival positively, but not any case of a negative influence (figure 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

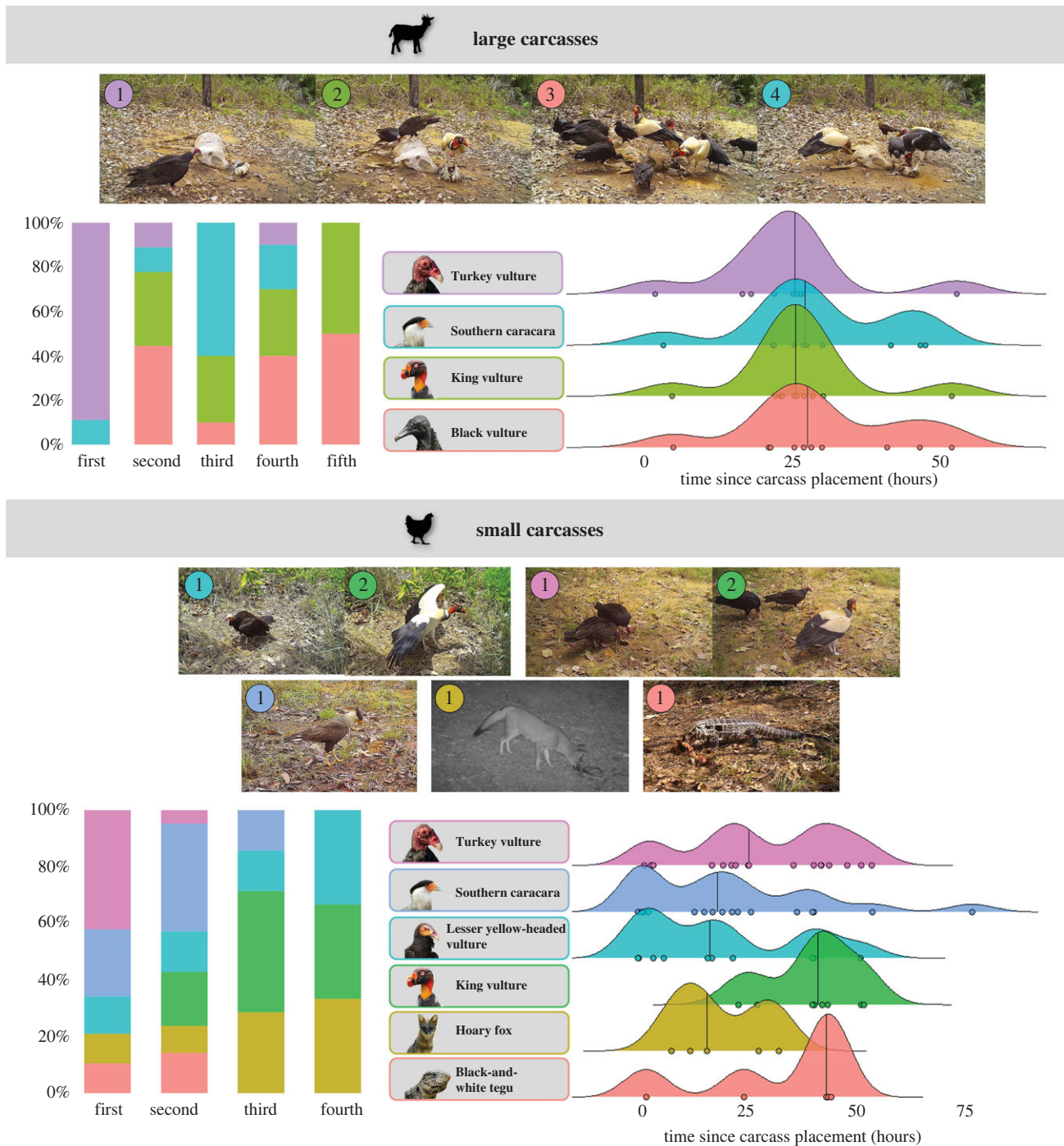


Figure 1. The succession of arrival (bar plots) and arrival time since carcass placement (smoothed plot) of different species to large carcasses and small carcasses. The photographs exemplify consumption patterns, numbers in each image refer to the chronological arrival of a new species and the colour 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 electronic supplementary material, table S2 for further details. (Online version in colour.)

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 figure 2 for these species). Furthermore, these results held whether we discretized the data to $\Delta t = 1$ min, $\Delta t = 10$ min or $\Delta t = 1$ h intervals, and whether we included or excluded the *time since carcass placement* in the baseline model (see electronic supplementary

material, 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 h, electronic supplementary material, table S2) had the highest effect, being included in the top-ranking models (green squares marked with thick borders in figure 2). Also at small carcasses, the lesser yellow-headed vulture (19.60 ± 18.43 h, electronic supplementary material, table S2) was influenced by the

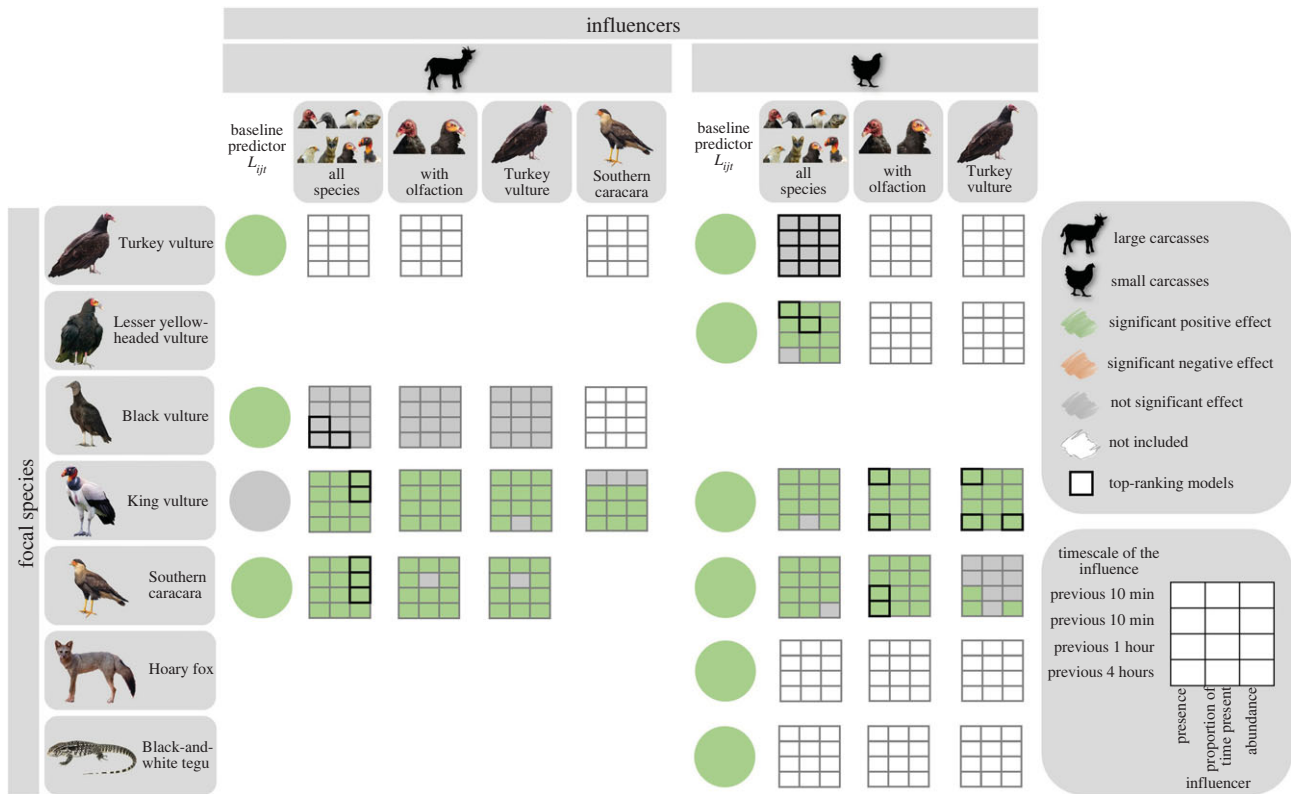


Figure 2. Results of the logistic regression on heterospecific influence on first arrival times, shown separately for large and small carcasses. Circles refer to the influence of the baseline predictor L_{ijt} , and the squares to the heterospecific influence. Positive and significant ($p < 0.05$) influence 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 electronic supplementary material, tables S3 and S4 for further details. The results are shown here for the data discretized to time resolution of $\Delta t = 10$ min, and for the case where the time since carcass placement was included in the baseline model. See electronic supplementary material, Information for corresponding results for data discretized to time resolution of $\Delta t = 1$ min or $\Delta t = 1$ h, and the case where the time since carcass placement was excluded in the baseline model. (Online version in colour.)

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; figure 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 electronic supplementary material, Information). We did not obtain any influence of heterospecifics on their arrival for turkey vultures, hoary foxes (19.13 ± 10.46 h) and the black-and-white tegu (31.45 ± 18.51 h), either because there were not enough previous occurrences of other species to fit the models, or because their influences were not significant (figure 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 (figure 2).

4. 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 (L Naves-Alegre, JA Sánchez-Zapata, E Sebastián-González 2018, 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 timescale by the different species, since some of them arrived at the carcass immediately upon perception

of the cue (e.g. 10 min) and others required longer periods of time (e.g. up to 4 h). 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 abilities among them [52,53]. We found that most species responded quickly to the previous presence of heterospecifics, which supports the 'local enhancement' hypothesis against the hypothesis of a wider chain of information (e.g. 'vulture chains' hypothesis) [41].

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

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

Data accessibility. All the raw data and analysis code used during the current study are available in the electronic supplementary material [54].

Authors' contributions. L.N.: conceptualization, data curation, formal analysis, investigation, methodology, resources, software, visualization, writing—original draft, writing—review and editing; Z.M.: investigation, methodology, writing—review and editing; J.A.S.: conceptualization, investigation, methodology, supervision, writing—original draft, writing—review and editing; E.S.: conceptualization, formal analysis, funding acquisition, investigation, methodology, project administration, supervision, validation, visualization, writing—original draft, writing—review and editing; O.O.: data curation, formal analysis, methodology, software, supervision, validation, visualization, writing—original draft, writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Conflict of interest declaration. We declare we have no competing interests.

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