

Foraging behaviour at carcasses in an Asian vulture assemblage: towards a good restaurant guide

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Summary

Vulture populations are declining steeply worldwide. Vulture ‘restaurants’ or feeding stations are a tool for maintaining and monitoring numbers, but individual species may be disadvantaged by the effects of carcass distribution, carcass size and interspecific aggression. To test the degree to which restaurants give opportunities for each species to access the food provided, we studied behaviour and morphology in three Critically Endangered species of vulture in Cambodia: the gregariously breeding and feeding White-rumped Vulture *Gyps bengalensis* and Slender-billed Vulture *G. tenuirostris*, and the solitary Red-headed Vulture *Sarcogyps calvus*. We video-recorded attendance time, attendance order and dominance behaviour at different-sized carcasses. Interspecific aggression at carcasses was least frequently shown by the ‘small’ White-rumped Vulture. The relatively ‘large’ Slender-billed and ‘medium’ Red-headed Vultures showed aggression more regularly and at similar levels. However, the latter avoids conflict by waiting until *Gyps* vultures are no longer crowding at the carcass, although its arrival at carcasses was correlated with total number of vultures present. While more numerous than Red-headed, the two *Gyps* vultures are more dependent on large carcasses, which increases their vulnerability to further declines in wild large ungulate species. Body size, number of individuals, hunger levels and carcass size and availability all influence carcass attendance behaviour. An increase in the number and spatial distribution of restaurants as well as of carcass size range could boost numbers of all vulture species.

Introduction

Populations of Old World vultures (family Accipitridae) are in deep crisis: of the 15 carrion-eating species distributed across eight genera in the tribes Gypini and Gypaetini, all but one have significant (‘Near Threatened’ or above) global threat status (BirdLife International 2014, del Hoyo and Collar 2014). The causes of this crisis include the declining abundance of wild animals on whose carcasses vultures depend, unintentional poisoning (either from drugs given to ailing cattle or from toxic chemicals laced on cattle carcasses to suppress mammalian predators, or lead intoxication), direct persecution (including poisoning of game carcasses by poachers to prevent vultures revealing their activities), and trade in body parts (Mundy *et al.* 1992, Collar *et al.* 2001, Cuthbert *et al.* 2006, Nam and Lee 2009, Gangoso *et al.* 2009, Hernández and Margalida 2009, Margalida *et al.* 2010, Ogada *et al.* 2012, 2015, Buij *et al.* 2015); for review on the effects on pharmaceuticals see Margalida *et al.* (2014).

An important conservation management response to this crisis has been the provision of drug- and poison-free carcasses at sites (‘restaurants’) which can be guarded from interference (Piper *et al.* 1999, Gilbert *et al.* 2007, Becker *et al.* 2009). Recently, restaurants have been established in Cambodia, where a small but important population of three ‘Critically Endangered’ species, Slender-billed Vulture *Gyps tenuirostris* (hereafter Slender-bill), White-rumped Vulture *G. bengalensis* (White-rump), and Red-headed Vulture *Sarcogyps calvus* (Red-head), persists

(Collar *et al.* 2001, BirdLife International Indochina 2005). Carcass surveys suggest that restaurants in Cambodia may increase available food supplies by up to 50% (Clements *et al.* 2012).

However, interspecific dominance hierarchies among foraging vultures play a key role in regulating access to carcasses: the gregarious ‘gulpers’ (including the two *Gyps* in this study), with long narrow bills, typically arrive first at a carcass, mostly in groups that exclude other vulture species; the more solitary ‘rippers’ (including the Red-head), with strong wide bills, feed later; and the ‘scrappers’, relatively small-billed and also solitary, pick items from and near the carcass (Kruuk 1967, König 1983, Hertel 1994, Houston 1995, Ferguson-Lees and Christie 2001). Disadvantages to particular species may, however, occur if the composition of a vulture community is in part shaped by carcass distribution (Wilmers *et al.* 2003, Blázquez *et al.* 2009), if carcass size plays a role in determining the number and proportions of vulture species feeding on it (Selva *et al.* 2005), and if aggression based on both group size and body size helps determine access to carcasses (Kruuk 1967, König 1974, Houston 1975, Kirk and Houston 1995, Carrete *et al.* 2010).

Clearly, therefore, when population sizes of all (and equally threatened) species in the vulture assemblage are very low, as in Cambodia, it is vital that the food provided at restaurants benefits all species. But how can this be achieved? One approach is to examine whether the amount and type of food provided produces asymmetrical benefits (Cortés-Avizanda *et al.* 2010, Kendall *et al.* 2012, Moreno-Opo *et al.* 2015). Another is to examine the behaviours that allow resource partitioning among vultures. Since methods of studying carcass exploitation involve considerable disturbance, including analyses of carcass composition and vulture intake during the feeding process, we chose the latter option, posing two main research questions:

- 1: What is the role of interspecific dominance and carcass size in carcass attendance order?
- 2: Is there interspecific aggression among individuals of the three species, and if so are outcomes of aggressive behaviour related to body size?

We used video recordings of vultures feeding at carcasses to answer these questions and, for question 2, supplemented this evidence with morphological data from museum specimens to describe body size.

Methods

Study site and experiment

The study was conducted at Siem Pang (UTM: 649256–1563359) and Seasan (UTM: 665298–1510843 (details in BirdLife International Indochina 2005) in the open, dry deciduous dipterocarp forests of the northern and eastern plains of Cambodia (Collar *et al.* 2001). Each site contained an already established restaurant located in open areas with only a few bushes and trees. At these restaurants one partially skinned cattle carcass was set out on eight occasions at two-week or greater intervals between December 2009 and April 2010. Newly exposed carcasses fell into two size categories, ‘large’ (over 100 kg), and ‘medium’ (50–99 kg). To assess reduction in size due to feeding, the carcass was weighed with a transportable spring balance 60 minutes after the last vulture finished feeding (if vultures were then still present, size class was visually estimated to avoid disturbance). A third category, ‘small’ (under 50 kg) was used for greatly reduced-size carcasses. Experiments were conducted in sunny weather, food exposure took place at 09h00 and video recording ran between 09h00 and 16h00.

Video data

A video camera (Sony HDR-SR11) was installed in an observation hide 20–30 m from the carcass to record all activities by each vulture species as soon as the carcass was set out. Distance between

carcass and video camera, angle and zoom were standardised to obtain comparable screen sizes. Zoom and thus screen size were standardised between videos to compare vulture numbers between sequences. When no vultures were present at the carcass the camera was stopped. Consequently we filmed a series of 5–8 sequences per carcass and a total of 49 sequences for all eight carcasses. Using only material with vultures present, we then produced eight ‘movies’ (one per carcass) of 1–6 hours in length, for a total of 2.4 hours of video of vultures feeding.

Morphology of museum specimens

To gauge whether body size is related to dominance hierarchy we measured wing length and tarsometatarsus length in 34 vulture specimens in the Natural History Museum, Tring, UK, involving 12 male Red-heads (Myanmar 2, Malaysia 2, Thailand 2, India 4 and Sikkim 2), 12 male White-rumps (Thailand 1, Nepal 1, Myanmar 5, India 5) and 10 Slender-bills (3 male, 1 female, 6 unsexed; India 6, Thailand 1, Malaysia 1, Nepal 1, Vietnam 1).

Carcass attendance data analysis

To understand the role of dominance and carcass size in carcass attendance order, we documented species presence and attendance time at the carcasses in videos. To track the order of attendance we chose only the first sequence per movie. Arrival and departure time of each individual Slender-bill, White-rump and Red-head was recorded, along with those of Himalayan Griffon *Gyps himalayensis*, a rare migratory visitor. We divided activity of vultures around the carcass into two spatial classes, first ‘IN’, to describe a bird’s activity either feeding or trying to do so directly at the carcass and within 1 m of it, and second ‘OUT’, to describe a bird’s activity when either queuing or sitting sated at least 1 m away from the carcass. We noted each individual arriving at or departing from the carcass in both categories IN and OUT, which we defined as an ‘event’. The number of vultures IN and OUT was assessed by the sum of all events in both categories. Thus we tracked a total of 3,819 events from the eight movies.

To avoid temporal autocorrelation in the data when recording a species IN or OUT we used only observations after the occurrence of 10 (for Slender-bill and White-rump) or 12 (for Red-head) events. In these data, temporal autocorrelation was negligible as assessed in the residuals from the model fits. We chose the data-thinning method over including temporal autocorrelation within the model because as yet there is no R-function to obtain the Bayesian joint posterior distribution of the model parameters from such models; moreover, when data are highly autocorrelated little information is lost by thinning. Owing to the small sample size of Red-heads at small carcasses all observations at small carcasses were omitted from this analysis (Figure 3). There remained 276 observations for analysing the presence of Red-heads and 382 for analysing the presence of Slender-bills, White-rumps and Himalayan Griffons.

We used R2.12 software package (R Core Team 2013) for all analyses. For analysing species presence we used the presence (0/1) IN of each vulture species as the dependent variable in a generalised linear mixed model with binomial error distribution and logit link function. The presence rather than the absolute number of individuals was used because the behaviour of a single vulture is probably mediated by the behaviour of other vultures nearby. Thus an independent count would be a group of vultures (not a single vulture). However, because the sizes of independent vulture groups were unknown we analysed presence/absence instead of absolute numbers.

As predictor variables we used time and included polygons up to the 4th degree, carcass size (medium and large categories respectively), the screen factor (value for ‘zoom-in’ factor) and the two-way interactions between all polynomials of time and carcass size. Sequence number and movie number were included as random effects in the model to account for repeated measures within the same movie, and sequence, respectively. To analyse Red-head presence, total numbers of each species IN and OUT were used as additional predictors. We built a set of candidate models following an information-theoretic approach based on AICc: (Burnham and Anderson 2002). A term was defined to be unimportant if the

AICc decreased by more than 2 units when it was deleted from the model. Unimportant interactions and polynomials were deleted stepwise from the model to ease interpretation of the remaining terms in the model, and to avoid overfit. We started with the highest order of interactions and polynomials. Main and linear effects were not removed. To assess model fit and check for assumption violation, residuals of the model were graphically plotted against fitted values. Quantiles of residuals were plotted against quantiles of normal distribution, and the raw and partial autocorrelations up to lag 25 were calculated. To analyse uncertainty of the model estimates and model predictions we used Bayesian methods to obtain uncertainty estimates of the model parameters as recommended for GLMMs (Bolker *et al.* 2008). For this we simulated 2,000 random sets of values from the joint posterior distribution of the model parameters using the function `sim` from the package `arm` (Gelman and Hill 2007). We defined an effect to be significant if zero is not included in the 95% credible interval.

Dominance and body size analysis

To assess dominance behaviour among individuals of the three species, we processed the videos for a second time but now with the focus on individual behaviour, following each individual in the sequences to note its aggressive interactions. Since interactions between vultures are most frequent in the first hours after exposing the carcass, we analysed the first three sequences of all eight movies; and to assess later activities at the carcass we randomly selected five later sequences from the movies. Thus, in total we analysed 29 sequences to assess interspecific interaction behaviour. To avoid double-counting individuals within each sequence, we followed (for a maximum of five minutes only) each diagnosable individual on screen from landing at the carcass until it disappeared into the crowd. We noted every behaviour that fits the patterns described below of either dominant or subordinate behaviour, using only every third interactive behaviour of each individual for analyses (to ensure independence of observations from subsequent fixed behavioural patterns). We grouped interactions between individuals into dominant and subordinate behaviours. The first group included (1) bite/strike with bill, (2) kick, (3) chase (pursuing and jumping at rival), (4) threat posture (wings open with neck down approaching rival), and (5) trampling rival. Subordinate behaviour involved being the target of (6) bites, (7) kicks, (8) chases, (9) threats and (10) trampling.

To assess differences in behaviour we grouped all single observations as either aggressive or subordinate behaviour. For each species we summed the total of all behaviours within each sequence. Differences in dominance behaviour between species were analysed using a binomial linear mixed model (GLMM). The number of dominant and subordinate behaviours per observation sequence was used as the dependent variable and species as the fixed predictor. Number of sequence (sequence-ID) was used as a random factor. We additionally included an observation-level random factor to account for overdispersion (Gelman and Hill 2007). Significances and fitted values with 95% credible intervals were obtained as described for the GLMMs above.

In total we analysed 1,670 observations in 29 sequences of all 10 behaviour patterns that were assigned to one of the five aggressive or subordinate behaviours. We recorded 1–28 individuals per species and sequence. We avoided double-counting and autocorrelation in each sequence, and assumed that geographic distance and time-lag between feeding events minimised the risk of tracking the same vultures at each feeding experiment.

Results

The highest numbers of individuals recorded simultaneously at a carcass were 35 Slender-bills and 40 White-rumps. *Gyps* vultures were always far more numerous at restaurants than Red-heads, for which only a maximum of six different individuals was recorded at one time. Himalayan Griffon occurred as a rare visitor (Figure 1).

The arrival of Red-heads directly to feed was positively correlated with the total number of vultures both IN and OUT (Figure 2). Although the *Gyps* vultures appeared soon after carcass deployment, they never landed directly at the carcass but assembled in trees and waited. By contrast,

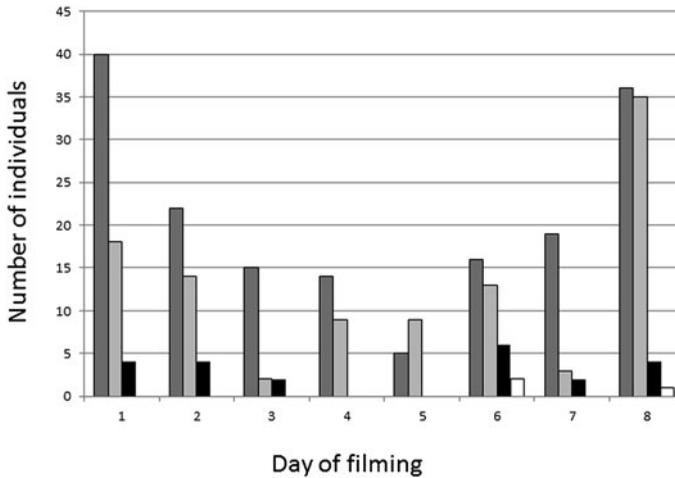


Figure 1. Maximum number of individuals per species simultaneously present at the carcass for each of the eight movies/days. Bars from left to right represent maximum numbers per video counted on the screen feeding and waiting to feed, by species and by day with bars representing White-rumps (dark grey), Slender-bills (light grey), Red-heads (black) and Himalayan Griffon (white). Days 1–8 were 16, 26 December 2009, 27, 28 January 2010, 9 February 2010, 3, 10, 16 March 2010.

in all movies the solitary Red-head appeared to be the first to move from OUT to IN. However, soon after a Red-head moved IN, as if this was a signal, both Slender-bills and White-rumps would go down to the carcass and start feeding in big groups. Presence probability of Red-head changed according to carcass size and time, with a significant interaction among these variables (Figure 3, Table S1 in the online supplementary material): it was low in the first two hours for both carcass size categories, but rose strongly after 2–3 hours at medium-sized carcasses. At large carcasses it dropped after around three hours (Figure 3). In contrast, presence probability of Slender-bill and White-rump IN was positively affected by carcass size, and thus was higher at

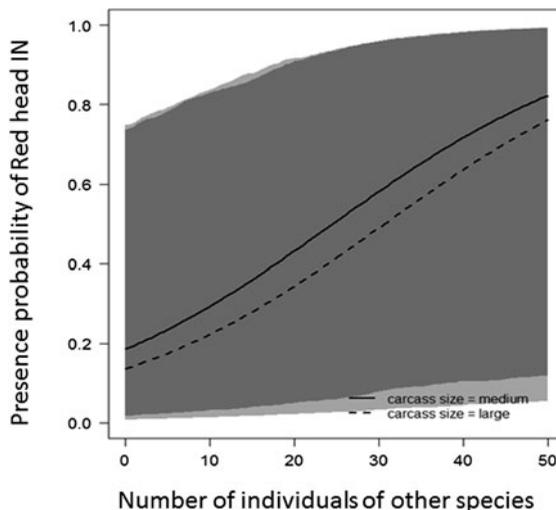


Figure 2. Presence probability of Red-heads feeding at the carcass in relation to the number of individuals of other species feeding. Shaded areas are the 95% credible intervals of the fitted values.

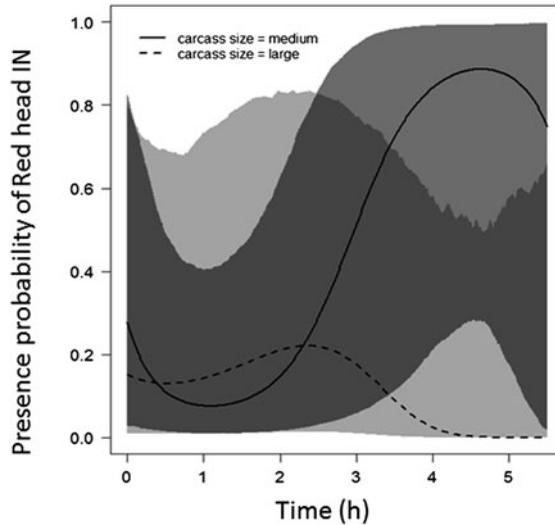


Figure 3. Presence probability of Red-heads feeding at the carcass over time for medium and large carcasses. Shaded areas are the 95% credible intervals of the fitted values.

large carcasses (Figure 4); it showed two peaks, one in the first 1–2 hours after carcass exposure and a second after around five hours (Figure 2).

Slender-bill proved the largest species (wing $578.5 \pm \text{SD } 11.3$, tarsus $101 \pm \text{SD } 2.1$), Red-head intermediate (wing $563.3 \pm \text{SD } 17.6$, tarsus $93.8 \pm \text{SD } 4$) and White-rump smallest (wing $547.5 \pm \text{SD } 11.6$, tarsus $87.9 \pm \text{SD } 2.5$), and this order was reflected in their dominance behaviour. White-rump had with 38% (CrI: 31–45%) a significantly lower proportion of aggressive interactions (bite, kick, chase, threat, trampling) than the other two species, with 62% (CrI: 50–72%) in Slender-bill and 60% (CrI: 51–68%) in Red-head. All species showed aggressive behaviour ranging between 25% and 47% of all observed interactions.

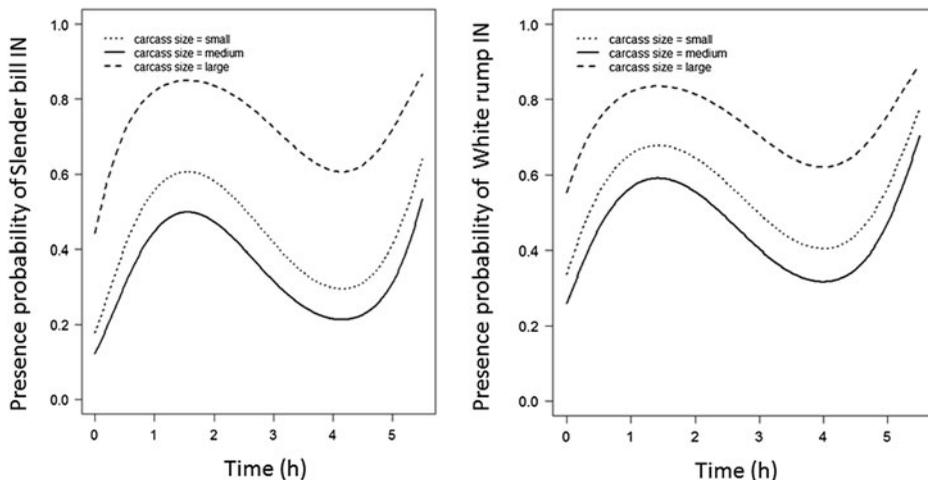


Figure 4. Presence probability of Slender-bill (left) and White-rump (right) feeding at the carcass over time for medium and large carcasses.

Discussion

Gyps species were almost 10 times more numerous at carcasses in Cambodia than Red-heads. Presence probability of Slender-bill and White-rump was highest at the start of feeding and at large carcasses, suggesting that these species are particularly sensitive to the quantity of food available in a given area (see also Moreno-Opo *et al.* 2015). Time of year evidently also matters: after the dry season, the starvation of many wild animals creates a peak in carcasses, resulting in higher numbers of vultures (Bunnat and Rainey 2009). Indeed, concentrations of *Gyps* species at restaurants in Africa and Europe vary with food availability (Blázquez *et al.* 2009, Cortés-Avizanda *et al.* 2012, Kendall *et al.* 2012, Moreno-Opo *et al.* 2015). Overall, our findings support the evidence that foraging behaviour in vultures at carcasses reflects a complex combination of spatial, temporal and social factors (see also Jackson *et al.* 2008, Deygout *et al.* 2010).

The facts that (a) the arrival of Red-heads at carcasses was correlated with total number of vultures present, and (b) Red-heads tended to feed before *Gyps*, triggering the *Gyps* into feeding and resulting in the Red-heads moving OUT, are intriguing. Ferguson-Lees and Christie (2001) also reported that Red-heads give way to arriving White-rumps and Slender-bills at large carcasses. This might be because the carcasses cannot be defended against high numbers of competitors, as in the case of adult and immature Common Ravens *Corvus corax* (Marzluff and Heinrich 1991), or because Red-heads, with their more powerful bills, are simply bolder in assessing ambush risk at carcass sites and are therefore used by *Gyps* vultures as advance guards. Only when *Gyps* vultures were sated and moved OUT did the more solitary Red-head access the now-reduced carcass and begin feeding (Figs. 3 and 4). Carcasses attended by large numbers of *Gyps* are presumably stripped down to a substrate more suited to Red-heads much faster than those attended by few *Gyps* individuals. We found higher presence probability of Red-heads at part-eaten medium-sized carcasses than at fresh large carcasses, suggesting their substrate specialisation.

Interspecific interactions were common in all three species while feeding, but differed significantly between species. As expected, dominance behaviour was related to body size. Predictably, White-rump exhibited the lowest dominant/subordinate ratio among the three species, with fewest aggressive interactions, but (rather less predictably) this appeared to allow it access to carcasses alongside the Slender-bill, although whether the two species avoided direct competition by consuming different body parts was not apparent.

African and South American vulture assemblages show a positive correlation between body size and interspecific dominance at carcasses (König 1974, Houston 1975, Carrete *et al.* 2010), but the measures used in these studies to describe body size (tail or bill length) rather reflect adaptations to food-searching and feeding than body size itself. Although dominance hierarchy is positively related to body size, aggression declines with satiation and seems part of a niche-partitioning process among species exploiting the carcass (see also König 1983). Younger subordinate and solitary birds tended to wait while aggregating *Gyps* species were feeding (consistent with findings in Bosè *et al.* 2012), and only fought for access to the carcass when the first sated *Gyps* moved away from it. Body size, number of individuals, hunger levels and carcass size and availability all evidently combine to affect the order in which species feed on carcasses.

Jostling and fighting at carcasses by animals with powerful hooked bills might be expected to produce serious injuries, but *Gyps* vultures depend so much on each other to find food (e.g. Cortés-Avizanda *et al.* 2014) that violent aggression would be self-defeating. Indeed, their evident preference for large carcasses suggests that overcrowding matters less than the apparently greater certainty of obtaining a meal, perhaps in part because they can better exclude potential rival scavenger species. However, the preference for or tolerance of crowding also suggests that the advantages of restaurants to *Gyps* species decline with declining size of carcass. If so, restaurants in Cambodia and elsewhere may need to provide large carcasses on a regular basis to optimise the chances of maintaining and indeed increasing existing *Gyps* numbers. Optimizing the functioning of supplementary feeding here means providing food regularly on a spatial and temporal basis (Moreno-Opo *et al.* 2015). Moreover, the Red-head's solitary behaviour, involving

well-spaced breeding sites, might mean that only a small proportion of its Cambodian population derives advantages from a regime of numerically low and/or spatially concentrated restaurants. To boost the survival prospects of all three species at this easternmost edge of their ranges, restaurants may therefore need to increase in number, size of carcass supplied and, crucially, spatial distribution. Indeed, evidence from Europe indicates that vulture species diversity (owing to an increase in dominant aggregating species and their learning effects) may decline when resources are concentrated in a few constantly used sites (Cortés-Avizanda *et al.* 2010, 2012).

Supplementary Material

The supplementary materials for this article can be found at journals.cambridge.org/bci

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