Scouts vs Usurpers: Alternative foraging strategies facilitate coexistence between Neotropical Cathartid Vultures

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Abstract

1. Understanding how diverse assemblages of scavengers can coexist on shared ecological resources is a fundamental challenge in community ecology. However, current approaches typically focus on behaviour at carcass provisioning sites, missing how important differences in movement behaviour and foraging strategies can facilitate sympatric species coexistence. Such information is particularly important for vultures - obligate scavengers representing the most endangered avian foraging guild. Their loss from ecosystems can trigger trophic cascades, mesopredator release, and disease outbreaks. 2. We use a combination of morphometric measurements and movement data from wild King (Sarcoramphus papa) and Greater yellow-headed (Cathartes melambrotus) vultures, coupled with carcass visitation data from animal carcass provisioning experiments to characterise scavenger community structure and strategies in the Peruvian Amazon. 3. King vulture body mass and tarsi length were larger (43% and 45% respectively), and tail shorter (22%) than the Greater-yellow headed vulture. King vultures also had substantially larger home ranges (˜500%), flew higher than Greater yellow headed vultures (695m vs. 360 m), and despite flying similar distances each day, were active later in the day. At carcasses, Greater-yellow headed vultures typically arrived first, but were rapidly outnumbered by both King and Black vultures (Coragyps atratus). 4. We find that the movement behaviour of obligate apex scavengers in the western Amazon is linked to their ability to coexist - the Greater -yellow headed vultures, a smaller stature 'scouting' species adapted to fly low and forage early, arrive first, but are ultimately displaced by larger-bodied king vultures at large ephemeral carrion resources. Expansion of future GPS tracking initiatives should facilitate the exploration of direct facultative interactions from animal movement data and give further insight into how diverse communities assemble and interact.

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Key words:

Movement ecology, obligate scavengers, traits, home range, flight, carcass, niche

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3. King vulture body mass and tarsi length were larger (43% and 45% respectively), and tail shorter (22%) than the Greater-yellow headed vulture. King vultures also had substantially larger home ranges (~500%), flew higher than Greater yellow headed vultures (695m vs. 360 m), and despite flying similar distances each day, were active later in the day. At carcasses, Greater-yellow headed vultures typically arrived first, but were rapidly outnumbered by both King and Black vultures (*Coragyps atratus*).

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Introduction

Diverse scavenger communities are essential for the maintenance of healthy ecosystems by rapid locating and removal of carcasses, thereby reducing the potential for the spread of diseases, stabilising food-webs and assisting in nutrient cycling (Gangoso et al., 2013; Craig et al., 2018; Carucci et al., 2022). Given the importance of scavenger communities, understanding the processes which allow for multiple species to coexist around carrion sites is paramount (Selva and Fortuna, 2007). Where species compete for high-value ephemeral resources, such as carrion, it may be expected that marked niche overlap drives high intra-species competition and low coexistence, ultimately resulting in low community diversity. However, a recent review highlights that carrion supports diverse scavenger assemblages worldwide (Sebastián-González et al., 2019), suggesting that mechanisms facilitating coexistence exist..

Several important mechanisms influencing scavenger community composition have been described. First, niche differentiation can occur in three principal ways: temporal, whereby species visit at different times in the diel cycle to reduce direct competition (Olea et al., 2022); spatial, whereby different sympatric species select habitats to minimise competitive interactions (Holland et al., 2019); or consumptive, whereby sympatric species consume different size classes of animal (Kendall, 2014). Second, facilitation related to how species locate carcasses can occur (e.g. through information transfer - Jackson et al., 2008; Williams and Safi, 2021), and according to how the resource is accessed (e.g. one species may open a carcass that other species can then exploit). Finally, competitive exclusion can also occur, which would result in negative co-occurrence of competing species at carcass sites (Carrete et al., 2010). Thus far,, the majority of research into processes which allow coexistence at carrion sites has focussed direct observations at carcass sites (e.g. using camera traps).

However such approaches alone cannot directly measureon how inter-species variation in movement behaviours promote sympatric species coexistence. Integrating carcass experiments within a movement ecology framework and connecting this with how their physiological traits shape such movements, will increase our understanding of sympatric species co-existence (Jeltsch et al., 2013).

Obligate vertebrate scavengers (vultures) are particularly important within terrestrial systems due to their capacity to rapidly remove large volumes of carrion. They possess unique adaptations (broad wings to efficiently glide, sharp vision, and, in some species, heightened smell) that enable them to quickly identify and consume carcasses (Ogada et al., 2012; Van den Heever et al., 2021). Vulture assemblages represent a valuable opportunity to understand mechanisms facillitating coexistence. In intact tropical ecosystems multiple sympatric species typically coexist within the same landscape and, as they are exclusively diurnal, diel separation in carrion visitation is not possible.Other mechanisms must predominate. It is thought that morphological characteristics (beak size, wing-span, talon length, etc), sensory capacities (e.g vision, smell (Grigg et al., 2017; Holland et al., 2017), movement strategies (Rabenold, 1987; Buckley, 1997), and feeding behaviour at carcasses, can facilitate coexistence (Hertel, 1994; Holland et al., 2019). However, coexistence is typically studied using static survey methods (such as camera traps) at carcass locations, making direct assessments of the role of movement strategies and traits difficult.

Alarmingly, vultures are facing major population declines globally - with 16 of the world's 23 vulture species threatened with extinction (Ogada et al., 2012; McClure et al., 2018). African, European, and North American vulture species have recently seen a rapid increase in research attention (Santangeli et al., 2022), the most dramatic declines to date have been detected in the Old World vultures, with some species declining up to 99% (Pain et al., 2008). In contrast, few studies have been conducted on vulture species within the Neotropics where deforestation, mining, and conversion of land for agriculture in the Amazon continue to increase. The Amazon forest is generally considered by many scientists to be approaching a "tipping point" of regional climate collapse leading to widespread biodiversity loss (Lovejoy and Nobre, 2019). The paucity of Neotropical data raises concern that without basic ecological information, the window for proactive cost-effective conservation strategies to avoid a collapse in Neotropical vertebrate scavenger communities will soon close (Santangeli et al., 2022). Understanding the ecology of these communities, how they coexist, interact with, and impact their surrounding habitat, is therefore critical.

To address the sparsity of integration between movement ecology and carcass provisioning experiments to date, and the general lack of information on neotropical vulture ecology, we adopt a duel vulture tracking and carcass provisioning approach to understanding scavengers community coexistence and structure within the Peruvian Amazon. For the movement component we focus on two poorly studied, sympatric, apex obligate vertebrate scavengers (Santangeli et al., 2022), the King vulture (*Sarcoramphus papa* - KV) and the Greater yellow-headed vulture (*Cathartes melambrotus* - GYV). Both are currently listed as 'least concern' on the IUCN Red List. However, King vulture populations are known to be declining generally and locally extinct at their most northerly range in Mexico and listed in CITES appendix III in Honduras (IUCN, 2016; *CITES*, 2022). To characterise the broader vulture community composition and interactions (King and Greater yellow-headed vultures are sympatric with black and turkey vultures within this landscape) we deployed large bodied (~50 kg) crcasses within the focal landscape and monitored species arrival and activity patterns with camera traps.

Specifically we: (1) Compare primary biometric traits between field-captured King and Greater yellow-headed vultures. (2) Using the latest solar GPS telemetry tags, analyse the movement characteristics of King and Greater yellow-headed vultures (average flight height, daily distance travelled, home range size, and time spent flying vs. non-flying). And (3), using camera trap monitored carcass drops to assess arrival timings of four sympatric Amazonian vultures (King and Greater yellow-headed, Black and Turkey vulture). We predict that: (1) King and Greater yellow-headed vultures will have different morphological traits. (2) That these traits will underpin different movement behaviours associated with differing foraging strategies. (3) that differences in traits and movement behaviours will be reflected in arrival times and activity patterns at provisioned carcasses.

Methods

Study area

Data collection was conducted between July 2021 and October 2022 in and around Los Amigos Biological Station, Peru (Figure 1). Los Amigos is located in Madre de Dios, Peru (12.56858° S, 70.09903° W) at an elevation of 200–300 m above sea level. It was established in 2000 and is protected by the Peruvian NGO Conservación Amazónica (ACCA). The mean annual precipitation is 2800–3000 mm, with a dry season from May to September. The study area contains two major forest types: *terra firme* terrace hardwood and floodplain successional forest and other shorter-lived vegetation associations, as well as *Mauritia* palm swamps and stands of *Guadua* bamboo. Hunting, gold mining, wood exploitation, road development, and slash-and-burn agriculture pose threats to the forest.

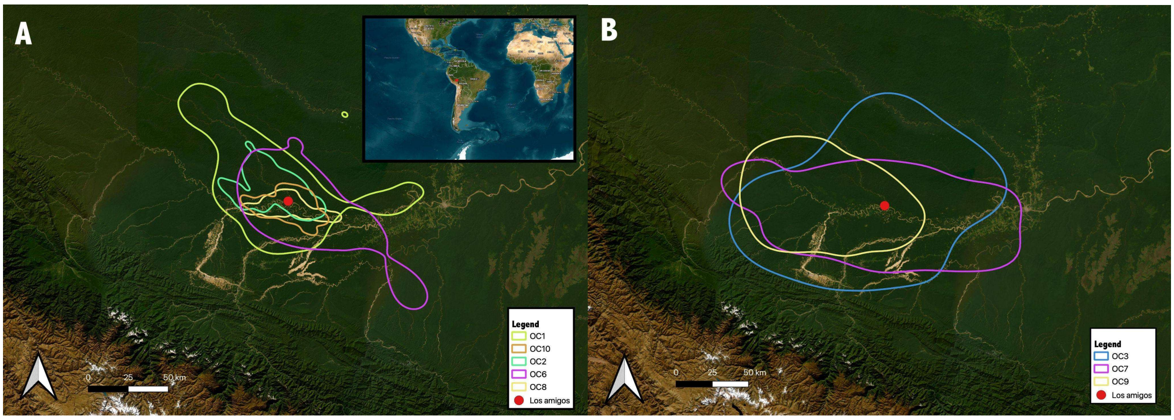

Figure 1: A map of the study site in the Peruvian Amazon with auto-correlated kernel density home-range estimators: Red dot = Los Amigos Biological Station; coloured lines = individual 95% kernel density home range estimates; **A =** Greater yellow-headed vulture; **B** = King vulture.

Capture and Tracking of Free-Ranging Vultures

Between July and August 2021 traps to capture vultures deployed and monitored. During the capture efforts, two walk-in, box-type traps (herein ‘traps’) were deployed side by side. These were built of steel tubes painted green for camouflage and closed with fishing net. The dimensions of the first trap were 2 m high x 2 m wide x 2 m deep, and of the door 2 m high x 1 m wide following the recommendations of (Barber and Bildstein, 2011), and the second trap had dimensions of 2 m high x 3 m wide x 3 m deep, and a door of 2 m high x 1.3 m wide. The swing-doors were activated by a rope leading to a hide 30 metres away to minimise disturbance. We used cow carcasses from the local slaughterhouse as bait.

We captured 10 individual vultures (King vultures [*Sarcoramphus papa*] = 5; Greater yellow-headed vultures [*Cathartes melambrotus*] = 5). We fitted eight individuals with e-obs (www.e-obs.de) light-weight, solar-panelled, GPS tags, which included a tri-axial accelerometer and altimeter (King vulture tag size 42g , n = 3; Greater yellow-headed vulture tag size 27g, n = 5); and two King vulture individuals were fitted with Northstar (https://www.northstarst.com) Phoenix solar-panelled, 40 g GPS satellite tags. These tags did not include altimeter and accelerometer. Tags were attached with a teflon harness and did not exceed 4% of the vulture’s body weight. The e-obs tags are fitted with GSM receivers, and when passing cellphone towers, data is downloaded to Movebank. e-obs tags were set to acquire locations every hour when battery levels were low and every 10 minutes when battery levels were high, from 5:00 a.m. to 19:00 p.m. local time. Phoenix tags collected hourly locations 24 hours a day with uplink via the Globalstar Satellite System.

As King and Greater yellow-headed vultures are sexually monomorphic, it was not possible to stratify tracking device deployment by sex. However, feather and blood samples were collected from captured individuals to perform sex determination via molecular methods *post-hoc*. Sex was determined via sex-specific DNA markers amplified by polymerase chain reaction (PCR). Using the ZymoBIOMICS DNA kit (Zymo Research), genomic DNA was extracted from blood preserved in FTA, filter paper, ethanol, and RNA later. Samples containing ethanol were heated at 45 °C for 10 minutes to evaporate the ethanol. After confirming the quality and amount of the genetic material, the DNA-binding chromo helicase gene associated to chromosomes Z and W (CHD-Z and CHD-W) was amplified using the GoTaq® Flexi DNA Polymerase Kit to amplify the DNA from each sample (Promega). In a T100 thermal cycler, PCR reactions were conducted with enzyme GoTaq® DNA Polymerase (5 U/L) from Promega (Biorad). For a final volume of 20 L, the following reagents were used: 1X buffer, $MgCl_2$ 1.5 mM, dNTPs 0.2 mM, primers forward (Fw) Yreverse (Rv) at 0.25 M, and GoTaq 1.25 U/rx. Initial denaturation at 95°C for 3 minutes, followed by 40 cycles of denaturation at 95°C for 30 seconds, annealing at 55°C for 30 seconds, and extension at 72°C for 25 seconds, with a final extension. 72 degrees Celsius for 5 minutes. The PCR products of the CHD gene were separated according to their molecular weight using 3% agarose gel electrophoresis and 15% polyacrylamide gel electrophoresis. The number of observed bands allows for the determination of the gender of the birds under investigation. The 50bp DNA Ladder (Thermo Fisher) used as a molecular weight marker has bands ranging from 50bp to 1000bp. After loading the samples onto the gel, they were run for 1 hour at 75V in the agarose gel and 2 hours at 110V in the polyacrylamide gel. To establish the gender of the birds, the CHD gene was amplified using the NP and 1272H primers, which produced a 258bp fragment for males and two 258 and 285-288 bp fragments for females in GYH. In contrast, for King vulture, the presence of two bands were not seen in any of the samples. Because of the different running patterns of the samples, it was determined to do the amplification using the pair of primers NP and P2, which amplified a 194bp fragment for males and two fragments of 194 and 215-224 bp for females.

All precautions and necessary care were taken to reduce potential discomfort or harm to the birds. The handling time was kept to a minimum to reduce stress. The weight of the transmitters and the method of fitting the device were carried out according to standard protocols and recommendations. A permit for equipping the vulture with the GPS transmitter, marking and collecting DNA samples was provided by Autorización del Servicio Nacional Forestal y de Fauna Silvestre (SERFOR), No AUT-IFS-2021-039, 18 June 2021.

Trait measurements

We measured morphometric data using standard measurements as described for vultures in (Mundy et al., 1992): (1) wing chord, from the carpal joint of the bent wing to the tip of the longest straightened primary; (2) bill length, from the tip of the culmen to the distal dorsal border of the cere; (3) bill width, at the level of the nostrils; (4) tarsus length, the distance from the tarso-metatarsal joint to the articulation of the middle toe; (5) tail length, from the insertion of the central rectrices to their tips; and (6) body mass. Callipers and a tape measure were used to take measurements to the nearest 0.1 mm. Digital precision scales were used to measure body mass to the nearest 0.01 g.

Carcass arrival monitoring

To explore the temporal dynamics of carcass discovery by different vulture species and wider scavenger community composition, we deployed six 50kg pig carcasses in the area surrounding Los Amigos Biological Station between the 7th of September 2021 and the 15th of March 2022. Carcass locations were selected based on accessible forest within 50m of the river banks. The area surrounding the carcass was cleared of small vegetation in a five metre radius from the centre point. Carcasses were monitored by two camera traps, one placed two metres from the carcass and one five metres from the carcass. Cameras were set to record a single image per motion trigger, with a quiet period of 10 minutes between successive triggers. Images were identified to species level manually in the Wildlife Insights camera trap management platform. We derived three metrics from the sequences of images for each of the four vulture species present in the region (King, Greater yellow-headed, black and turkey vultures): i) arrival order - defined as the order in which each vulture species was first detected at a given carcass; ii) arrival time in daylight hours - defined as the number of daylight hours (0600-1800 as vultures do not typically fly at night) which elapse between carcass deployment and their first detection on a camera trap; and iii) the proportion of images which contain each given species each hour.

Data analysis

i) Biometric comparison

As we have a single measure from each individual, we used linear models with the trait of interest as the response terms (weight, wing span, tail length, beak width, beak length and tarsus length) and species is the explanatory variable. Significant differences between the species were assessed using ANOVA using a 0.05 threshold.

ii) Movement characteristics

The movement data analysed here were collected between the 10th of July 2021 and the 31st of October 2022, which represented 156,704 locations. Six of the trackers functioned for the full survey duration, four failed beforehand, giving a mean number of collection days per individual = 357 (range = 40 - 488). Because of small sample sizes, data for males and females were combined for all analyses. We visually inspected tracks to check for any implausible locations arising through location error (we found none). Then the data were filtered to remove segments with implausible speeds (>100 kmph - the top reported speed for similar vulture species) between successive fixes, resulting in the removal of a single data point. For movement characteristics which required regularised data to avoid bias arising from sampling frequency (daily distance travelled and behavioural state models), we accounted for missing and irregularly timed location data by fitting a continuous time-correlated random walk (CRAWL) model (Johnson et al., 2008, 2022), to predict locations at 1-hour intervals. This resulted in a dataset containing 74,992 locations. As the CRAWL models do not function well where location data are sparse, we further filtered the regularised data to censor any days where we had location information for fewer than 10 of 12 daylight hours, resulting in a final dataset size of 67,451 locations.

For all individuals with > 200 days of raw tracking data (n = 8), we calculated home-ranges using Auto-correlated kernel density estimate (AKDE) function with the default parameters of the ‘ctmm’ package (Calabrese et al., 2016; Fleming and Calabrese, 2017). The AKDE estimator takes auto-correlated data and limited sample sizes into consideration. Variograms were constructed for each individual to determine if home-range behaviour was shown. Variograms depict the average square distance travelled by an individual over specified time intervals (termed semi-variance). Using the variograms, we visually verified if an individual's motions indicated range residence (a flattening of the semi-variance values), a necessary assumption for calculating home ranges with AKDEs (i.e., vultures remain within their home range areas, and do not exhibit nomadic or migratory behaviours). Then, various movement models (continuous-space and continuous-time stochastic movement models) contained in this package (Calabrese et al., 2016) were separately fitted to each individual. According to Akaike's information criterion (AIC), the best models were chosen and used to fit the 95%

AKDE. Differences between home-range sizes were analysed using quasi-poisson generalised linear mixed effect models.

The daily movement (km) was calculated by summing the straight-line distances between successive locations on the same day using the regularised vulture movement dataset described above (hourly intervals). Differences in distance travelled were analysed with generalised linear models using the ‘lme4’ package in R (Bates et al., 2015).

For all the individuals with tags which collected height information (n = 8), flight height was calculated following (Poessel et al., 2018). Geoid undulation values were calculated for each GPS point using the Earth Gravitational Model 2008 (Pavlis et al., 2012), downloaded from: https://www.unavco.org. We then subtracted the geoid undulation values from the height above ellipsoid (recorded by the e-obs tags) to obtain Altitude above sea level (ASL). Finally, the ASTER Global Digital Elevation Model (sourced from www.geogpsperu.com) for our study area was imported into QGIS, and ground elevation was extracted for each GPS point and subtracted from the altitude ASL to estimate Altitude above ground level (AGL). After a visual inspection of the Altitude AGL, we retained altitude values from 0 m - 2000 m AGL which resulted in the removal of four values which likely arose due to errors (Appendix A). To ensure locations collected were only from flying vultures, we removed any locations with altitudes lower than 30 m. To compare average daily maximum flight heights between species, we used a linear fixed effect model with daily maximum flight height as the response term and individual ID as a random intercept term to account for repeated measurements.

iii) Path segmentation analysis

To classify differing movement behaviours (flying vs. non-flying), we implemented Hidden Markov Models (HMM) using the ‘moveHMM’ R package (Michelot et al., 2016) on the regularised (hourly) vulture movement dataset. HMMs use movement elements (step-lengths and turning angles) to predict behaviour from known GPS points, and the probability of behavioural state change when reaching the next location. These methods can distinguish resting/feeding vs active phases (such as travelling and foraging). We fitted a 2-state no covariate model to both vulture species. HMMs require starting values for step lengths and turning angles, for our analyses we used a function in R which uses a suite of starting values and returns the best fitted model. These were checked and the lowest AIC model was used. Last, we fitted our model and assigned behavioural states using the Viterbi algorithm, which formulates the most likely state sequences (Zucchini et al., 2016), then the proportion of time spent resting/feeding vs. travelling/foraging were compared between the species using linear mixed effects models.

iv) Carcass arrival patterns

To explore temporal patterns in carcass visitation we created single species binomial mixed effects models with the proportion of images of each given species detected per hour as the response term, and daylight hours since carcass deployment as linear and quadratic terms and carcasses deployment code as a random intercept term (to account for repeat measures from the same carcass). We compared the linear and quadratic time models with the null model based on AICc, and only present the results from the best supported model.

Results

i) Biometric comparisons

There were significant differences between King vultures and Greater Yellow-headed vultures for three of the six traits assessed (Figure 2). King vultures were, on average, 2 kg heavier (43%; Figure 2A), had tarsi ~30 mm larger (45%; Figure 2F), and a tail that was 4 cm shorter (22%; Figure 2C) than the Greater yellow-headed vultures. We found no significant differences between wing-span (Figure 2B), beak length (Figure 2E), or beak width (Figure 2D).

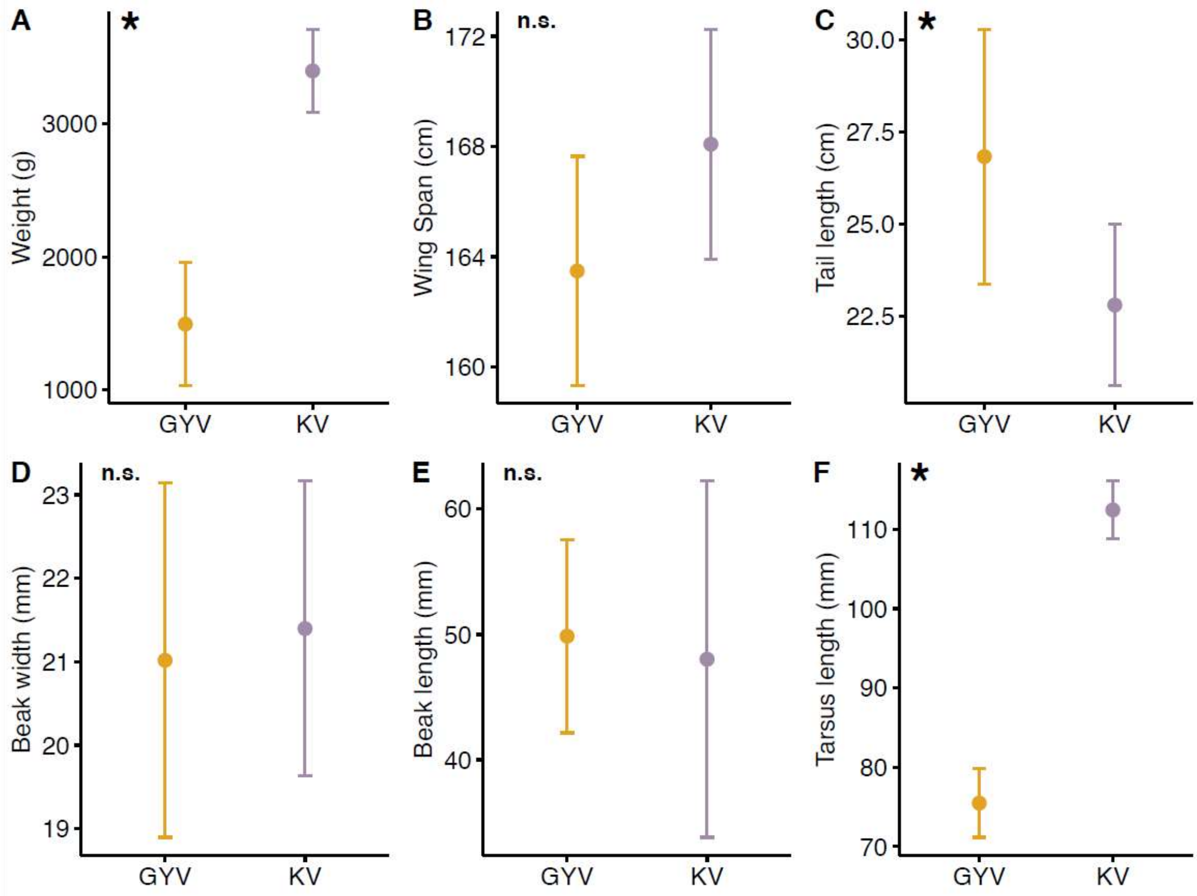

Figure 2: Error-bar plot of King vulture (KV) and Greater Yellow-headed vulture (GYV) morphometric measurements (A = weight (g); B = wing span (cm); C = Tail length (cm); D = beak width (mm); E = beak length (mm); F = Tarsus length (mm). Where: points = species-specific mean values; vertical lines = 95% confidence intervals; * = significantly different between species; n.s. = not significantly different between species. Raw morphometric data are shown in Appendix B.

ii) Movement characteristics

The home range of the King vulture was estimated to be five times larger than that of the Greater yellow-headed vulture (Figure 3A; 2750 km2 vs. 13,000 km2). Despite these differences there was no statistically significant difference in the average daily distance travelled by each species, although King vultures travel an average of 10 km less than Greater yellow-headed vultures each day (Figure 3B; 28 km vs. 40 km) - suggesting daily travel distance is highly variable. The average daily maximum flight height was significantly higher for King vultures than Greater yellow-headed vultures (Figure 3C; 695 m and 360 m respectively), the differences were not driven by physiological maxima as the maximum recorded heights of each species were similar (King vulture = 1983 m; Greater yellow-headed vulture = 1729 m). There was also support for species-specific diel flight height patterns (Figure 3D), where King vulture average flight heights peaked at around midday (~592 m), whereas Greater yellow-headed vulture flight height increased steadily until the midafternoon (~160 m).

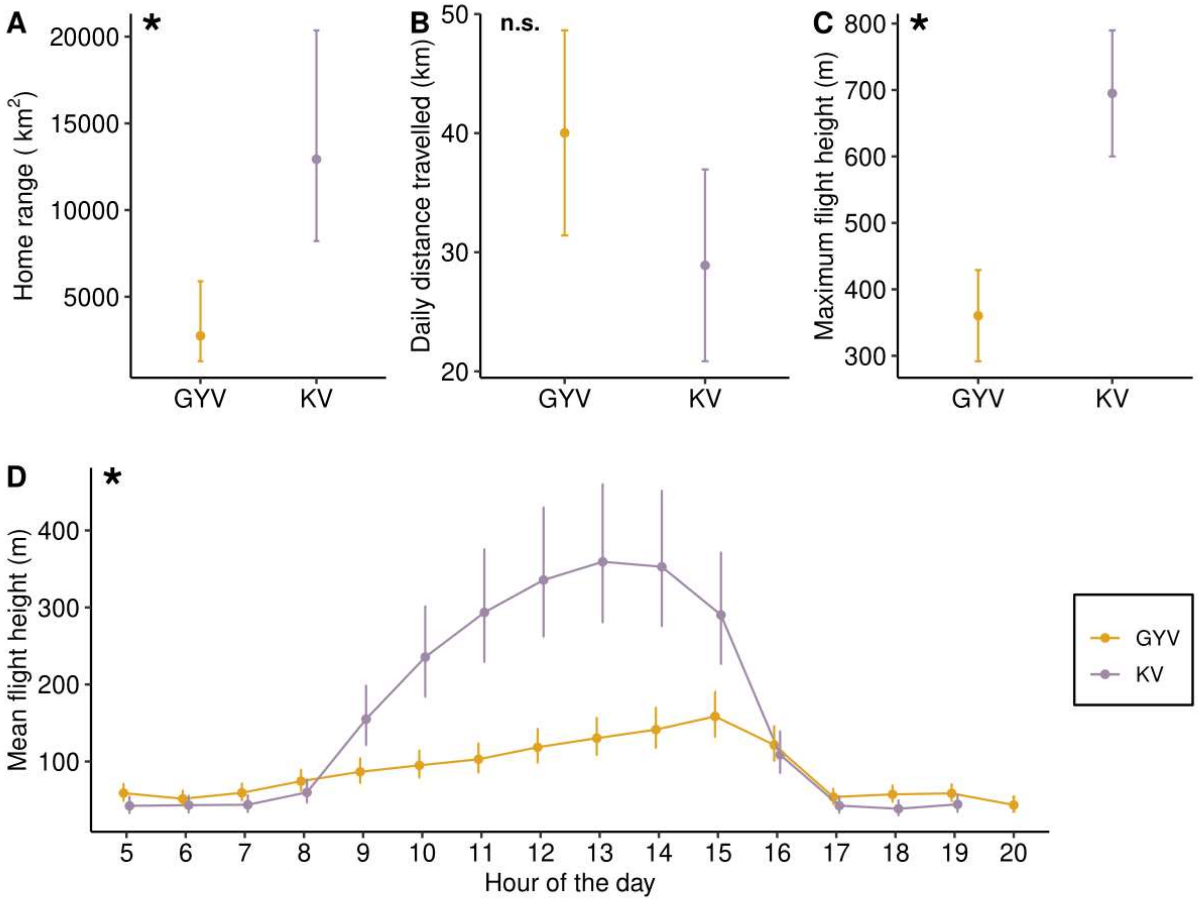

Figure 3: A = Estimated home range (km^2); B = average daily distance travelled (km); C = estimate daily maximum height (m); D = Estimated hourly height (m). Where: points = species-specific mean values; vertical lines = 95% confidence intervals.; * = significantly different between species; n.s. = not significantly different between species. Raw movement characteristics data are shown in Appendix C.

iii) Path segmentation analyses

The behavioural model (flying vs. non-flying) demonstrated that although King vultures and Greater yellow-headed vultures spend a similar proportion of each 24-hour period flying (~25%; Figure 4A), when these flight times occur differ during the day, the probability that Greater yellow-headed vultures are flying is significantly higher than King vultures in the late morning (9 am and 10 am) whereas King vultures remain in flight later into the evening (6 pm and 7 pm).

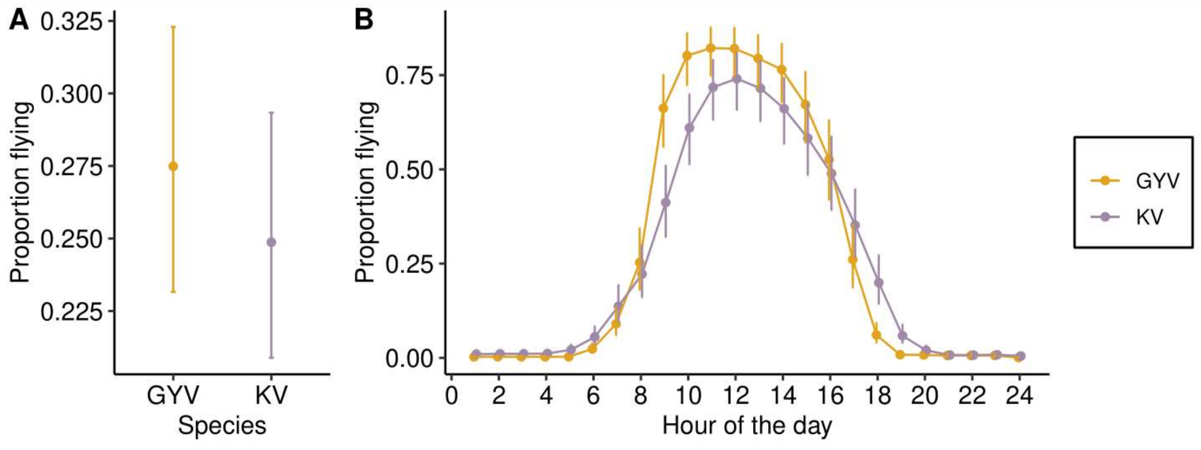

Figure 4: The estimated proportion of hourly observations where the individual is flying across all time steps (A) and through different hours of the day (B). Where: points = species average from a linear mixed effects model; vertical lines = 95% confidence intervals.

iv) Carcass arrival times

Camera trap monitoring of provisioned carcasses revealed that of the four vulture species which arrived to feed, three visited all carcasses (King, Greater yellow-headed, and black vultures) and Turkey vultures were detected at two of the six (33%). Greater yellow-headed vultures were the first species to be detected at the animal carcass in 3 out of 6 occasions (50%), and second in the remaining 50% of cases (Figure 5A) with the shortest average time until detection (5.3 daylight hours). Black vultures were first to be detected at 2 of 6 carcasses (33%) with the second shortest time until detection (6.6 daylight hours). King vultures were typically detected after Greater yellow-headed and black vultures, third at 5 of 6 carcasses (83%), and first on one occasion. They also had the second longest average time until detection (12.8 daylight hours). Turkey vultures, if detected, were the last to arrive (4th), and had the longest average time until detection (17.5 daylight hours). The proportion of images containing a given species showed marked interspecies variation: Greater yellow-headed vultures were, on average, the dominant species in the first 10 daylight hours from carcass deployment, then replaced by king and black vultures as time increased. As the relative number of detections of king and black vultures began to fall again (~40 hours), the relative abundance of Greater yellow-headed vultures again began to rise. Turkey vultures were infrequently detected across all times.

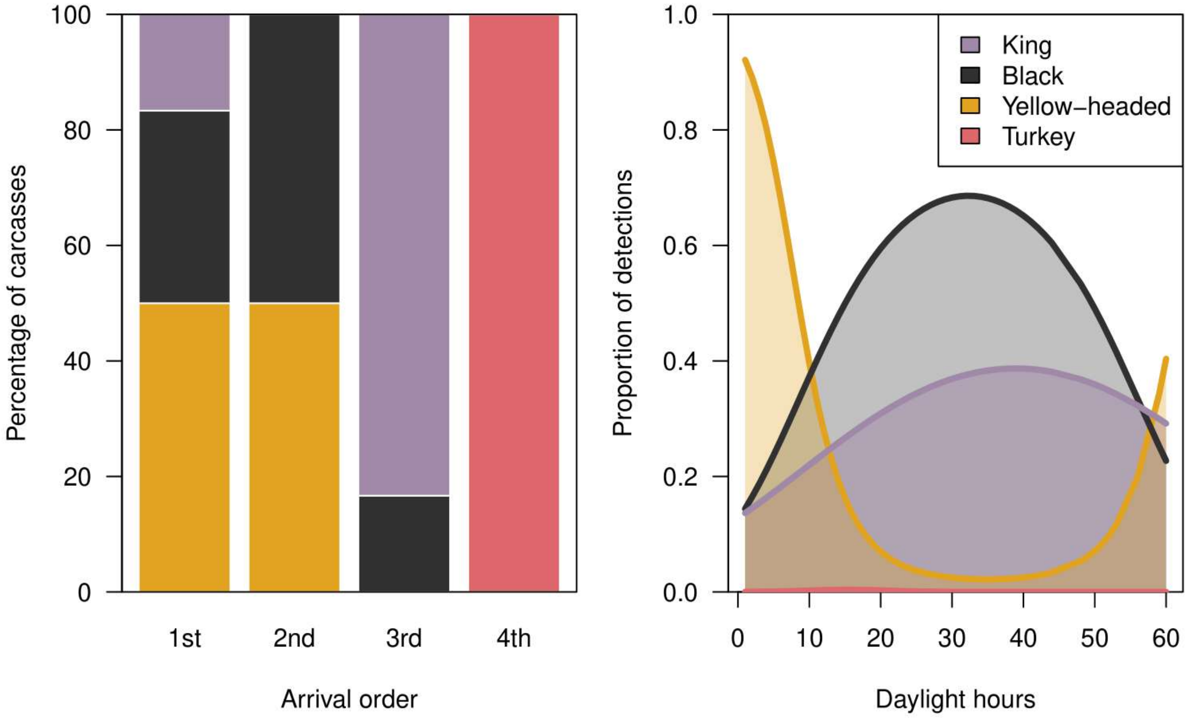

Figure 5 Summary of arrival order (A) and the predicted proportion of detections through time (B) for each of the vulture species detected. Where: "Arrival order" represents the order at which species were detected at provisioned carcasses; 'proportions of detections' represents the mean estimated proportion of detections of a given species from single-species mixed-effects model; and 'daylight hours' represents the number of daylight hours since carcass deployment.

Discussion

Here we use a complementary set of approaches and technologies, including morphological measurements, data from on-bird sensors, and camera trap-gathered carcass interaction data, to differentiate the foraging strategies of King and Greater yellow-headed vultures (Naves-Alegre et al., 2022). We find several clear differences in physical traits associated with flight behaviour (weight, wingspan, and tail length) and feeding (tarsus size), marked differences in space use and flight behaviours related to foraging, and corresponding differences in carcass arrival time and temporal feeding patterns. Below, we discuss how these findings provide insight into how multiple obligate scavengers can coexist and compete for high-value ephemeral carrion resources, and discuss the implications for the future protection of diverse scavenger networks.

Elucidating the mechanisms by which diverse assemblages of competing species can persist is a fundamental challenge in community ecology. In the case of obligate scavengers, the spatio-temporal unpredictability of high-value ephemeral resources such as carrion, allows species with alternative foraging and feeding strategies to coexist (Cortés-Avizanda et al., 2012). Interestingly, the sympatric King and Greater yellow-headed vultures show no overt differences in beak morphology, which suggests they have the potential to consume similar food items, perhaps indicating that the type of carrion resource utilised plays a relatively minor role in niche differentiation of these species. Rather, these species adopt differing search strategies. The combination of traits and movement behaviour of Greater yellow-headed vulture is consistent with foraging scouts - they are relatively light-weight, start flying in the early morning, low over the canopy and across relatively small home ranges. These traits, in combination with Greater yellow-headed vulture's well developed sense of smell (Luis G. Gomez et al., 1994) means that they are typically the first vulture species to 'smell-out' potential food sources and arrive at a carcass. The King vulture, in contrast, adopts a different approach - weighing over double that of a Greater yellow-headed vulture, they start flying later in the morning, fly higher and across huge home ranges. Given King vulture's relatively poor sense of smell (Houston, 1984), these physical and movement traits reflect visual searching for food within the landscape. While it has been suggested that King vultures specifically look for and follow jaguar (*Panthera onca*, Schlee, 2007), in closed canopy forest such as the lowland amazon direct visual sightings of predators or carrion are likely rare. Indeed, other studies outside of the Neotropics have found that vultures tend to prefer carcasses not killed by predators (Kendall et al., 2012). The visual cues they are using are more likely to be signs of other birds, like the Greater yellow-headed and Turkey vultures, but most likely by the mass flocks of Black vultures that begin to swarm any carcasses initially discovered by the Greater yellow-headed vulture. Relative to the Greater yellow-headed vulture, there is less of an advantage for King vultures to find carcasses first as they are able to use their large size to competitively displace smaller species from carrion when they arrive (Naves-Alegre et al., 2022).

Consistent with the morphological and movement trait data, we find no evidence of spatial niche separation between King, Greater yellow-headed and Black vulture at provisioned carcasses - they were detected at all provisioned carcasses. Rather, species differed in their temporal patterns of carcass visitation. King and Black vultures tend to get longer feeding-times as the dominant species at carcasses (~50 daylight hours), whereas Greater yellow-headed vultures accessed the food resource earlier, and for a shorter time period (typically within the first 10 daylight hours). Greater yellow-headed vulture did often remain in the vicinity of the carcass, and after 50 hours, would become the dominant species at carcasses once again - suggesting that they can utilise older carrion, or that they specialise in cleaning up remaining sinew and cartilages left by the King and Black vultures. Interestingly the Turkey vulture was only detected at one of the six carcasses, suggesting either some element of spatial niche separation, or perhaps a preference for very recently deceased carrion. Previous work has shown that Tukey vultures were efficient at detecting day-old carcasses, and would reject extremely rotten meat (Houston, 1986).

There are two key limitations to this study that would be fruitful to address in future research. The first relates to our chosen size of provisioned carcasses - we used relatively large pig carcasses (~50kg) to mimic carcasses of larger rainforest vertebrates, such as peccaries, tapir, or capybara. However, it has recently been shown in the Brazilian *cerrado* (Naves-Alegre et al., 2022) and in African regions (Kendall et al., 2012), that different sized carcasses contribute to the resource partitioning of vultures. Perhaps smaller carcasses are quickly discovered by Greater yellow-headed or Turkey vulture which have the greatest sense of smell and 'scouting' ability, and feed before large aggregations of King or Black vultures can form and displace them. Previous research suggests there is also potential for spatial niche separation according to habitat type (Holland et al., 2019) which may contribute to the coexistence of neotropical obligate scavengers. Whereas Greater yellow-headed vultures may typically arrive first to carrion located in dense closed-canopy forest, carrion in open habitats (e.g. riverine or cattle pasture) may be more readily accessible to the fast detection by the visual Black or King vultures. Each of our provisioned carcasses were beneath a closed forest canopy. Future work should investigate this effect of carcass size and stratifying between different habitat types to gain a more complete picture of the mechanisms promoting coexistence in neotropical vulture communities.

Our biometric and movement data is limited by a relatively small sample size of birds. However, they represent the first GPS tagged individuals of either species (King and Greater yellow-headed vulture) to be published. Expanding the tracking initiatives to more individuals, throughout a broader set of habitats, and in locations with and without sympatric species, would allow assessments of context dependent foraging behaviours. Furthermore, a greater number of tracked individuals in the same focal landscape would facilitate assessment of information transfer and interactions between vulture species directly from their movement behaviour (e.g. Long, 2015; Williams and Safi, 2021; Nathan et al., 2022). Increasing the sample sizes within and across species will also help understand how individual movement and behavioural decisions scale up to influence community processes (Costa-Pereira et al., 2022). Perhaps the most pressing need from a conservation perspective, is to study how human modification influences the mechanisms of coexistence in the neotropical obligate scavenger communities (Santangeli et al., 2022). For example, research from southern Argentina (Carrete et al., 2010) suggests that the common Black vulture, a generalist and disturbance tolerant species, appears to be expanding its range alongside increasing human development, potentially increasing competitive and antagonistic interactions with threatened Andean condor (*Vultur gryphus*). As anthropogenic disturbance expands in the Amazon, negative responses of other species thought to depend on contiguous undisturbed habitats (e.g. Greater yellow-headed or King vulture) could ultimately lead to decreased diversity and homogenization, with potentially negative consequences for ecosystem functioning of neotropical ecosystems.

Conclusions

We have shown how integrating methods and technologies can elucidate mechanisms of coexistence in neotropical obligate scavenger communities in a remote, natural ecosystem. Vultures adopt different foraging strategies in the absence of overt spatial and diel niche separation, which influence when and how they find high value ephemeral resources. The crucial next steps are to determine how expanding human modification will influence the movement decisions, interactions and information transfer between different obligate scavengers, and the implications of such changes on the vital ecosystem services they provide.

Ethics declarations

This study involved the capturing and handling of wild animals. To ensure the safety and welfare of both the wild animals and the field team this research study project followed already established protocols for the capturing and handling of large raptors (vultures). These protocols were carried out by experienced and trained wildlife veterinarians and biologists to ensure the health and safety of the animals. Personal Protective Equipment (PPE) was always utilised by the field team as part of the biosecurity protocols to ensure there was no possibility of transfer of virus or disease between wild animals and people. Finally, all GPS harnesses deployed on vultures followed the established rule of not weighing more than 4% of the bird's body weight to ensure the bird is healthy post-capture and there are no factors reducing the survival of the bird.

Consent for publication

Not applicable.

Competing interests

The authors declare that no competing interests exist.

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