


Scouts vs. usurpers: alternative foraging strategies facilitate coexistence between neotropical Cathartid vultures

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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. We provide the first-ever analyses of GPS location data from wild King Vultures *Sarcorampus papa* and Greater Yellow-headed Vultures *Cathartes melambrotus*, coupled with trait data (from both wild-living and museum specimens) and visitation data from camera traps deployed at provisioned carcasses, to characterize vulture flight behaviour and strategies in the Peruvian Amazon. We found marked species differences in several key movement characteristics, including: King Vultures having home-ranges five times larger, average flight heights four times greater and ground speeds 40% faster than those of Greater Yellow-headed Vultures. Despite these differences, both species flew similar distances each day (on average), probably due to King Vultures taking 50% fewer flights and spending 40% less time in the air per day. Consistent with these patterns, King Vulture body mass was more than double that of the Greater Yellow-headed Vulture, with a substantially larger hang wing index (a measure of long-distance flight efficiency). At carcasses, Greater Yellow-headed Vultures typically arrived first but were rapidly outnumbered by both King and Black Vultures *Coragyps atratus*. We find that the movement behaviour of obligate apex scavengers in the western Amazon is linked to their ability to coexist – Greater Yellow-headed Vultures, a smaller stature ‘scouting’ species adapted to fly low, forage early and arrive first at carcasses, are ultimately displaced by larger-bodied, wider ranging King Vultures at large ephemeral carrion resources. Expansion of future GPS tracking initiatives could facilitate the exploration of direct facultative

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interactions from animal movement data and give further insight into how diverse communities assemble and interact.

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Diverse scavenger communities are essential for the maintenance of healthy ecosystems by rapidly locating and removing carcasses, thereby reducing the potential for the spread of diseases, stabilizing 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 for ecosystem functioning, understanding the processes that allow for multiple species to coexist around carrion sites is paramount (Selva & Fortuna 2007). Where species compete for high-value ephemeral resources, such as carrion, it may be expected that marked niche overlap drives high intraspecific 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 minimize competitive interactions (Holland *et al.* 2019); or consumptive, whereby sympatric species consume different size classes of animal (Kendall 2014) or different parts of the same carcass (Hertel 1994, Moreno-Opo *et al.* 2016, Böhrer *et al.* 2020). Secondly, facilitation related to how species locate carcasses can occur (e.g. through information transfer – Jackson *et al.* 2008, Williams & 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 that allow coexistence at carrion sites has focused on direct observations at carcasses (e.g. using camera traps; Moreno-Opo *et al.* 2016, Mateo-Tomás *et al.* 2019, Naves-Alegre

et al. 2022a, 2022b). However, such approaches alone cannot directly measure how interspecific variation in movement behaviours can promote sympatric species coexistence. Integrating carcass experiments within a movement ecology framework and connecting the patterns observed with the physiological traits linked to such movements will increase our understanding of species coexistence (Jeltsch *et al.* 2013).

Vultures are particularly important within terrestrial systems due to their capacity to remove large volumes of carrion rapidly. They possess unique adaptations (including broad wings to efficiently glide, sharp vision and, in some species, heightened olfactory ability) that enable them quickly to identify and consume carcasses (Ogada *et al.* 2012, Van Den Heever *et al.* 2021). In intact tropical ecosystems, multiple sympatric species typically coexist within the same landscape and, as they are near exclusively diurnal, diel separation in carrion visitation is not possible. Other mechanisms must predominate. It is thought that morphological characteristics (e.g. beak morphology and wing-span; Hertel 1994), 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 (e.g. arrival timing – Kendall *et al.* 2012; activity patterns – Naves-Alegre *et al.* 2022a, 2022b; and agonistic interactions – Moreno-Opo *et al.* 2020) facilitate their coexistence.

Alarmingly, vultures are facing major population declines globally – with 16 of the world's 23 species threatened with extinction (Ogada *et al.* 2012, McClure *et al.* 2018). 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). African, European and North American vulture species have recently seen a rapid increase in research attention (Santangeli *et al.* 2022). In contrast, few studies have been conducted on vulture species within the Neotropics, where deforestation, mining and conversion of land for agriculture continue to increase. The Amazon is generally considered by many scientists to be approaching a 'tipping point' of regional

climate collapse leading to widespread biodiversity loss (Lovejoy & Nobre 2019). The paucity of Neotropical data raises concerns 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 dual vulture tracking and carcass provisioning approach to understanding scavengers' community coexistence and structure within the Peruvian Amazon. For the movement component we focus on GPS tracking of two poorly studied, sympatric, apex obligate vertebrate scavengers (Santangeli *et al.* 2022): the King Vulture *Sarcophaga 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, are locally extinct at their most northerly range in Mexico and are listed in CITES appendix III in Honduras IUCN 2023. To characterize the broader vulture community composition and interactions (King and Greater Yellow-headed Vultures are sympatric with Black *Coragyps atratus* and Turkey *Cathartes aura* Vultures within this landscape) we provisioned large bodied (~ 50 kg) carcasses and monitored species arrival and activity patterns with camera traps.

Specifically we: (1) use the latest solar GPS telemetry tags to compare and contrast a suite of movement characteristics of King and Greater Yellow-headed Vultures (including home-range, and daily, flight bout and individual location characteristics); (2) link the movement traits observed to species-specific biometric traits; and (3) use camera traps to monitor arrival timings of the four sympatric Amazonian vultures (King, Greater Yellow-headed, Black and Turkey Vultures). We predict that: King and Greater Yellow-headed Vultures will display different flight characteristics consistent with variation in key morphological traits, and that such differences will be reflected in species-specific 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 (Fig. 1), located in the Madre de Dios region (12°34'6.89"S, 70°5'56.51"W) at an elevation of 200–300 m above sea level. Los Amigos was established in 2000 and is protected by the Peruvian NGO Conservación Amazónica (ACCA). 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, 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 wider region.

Capture and tracking of free-ranging vultures

All of the individuals within this study were captured between July and August 2021. During the capture efforts, two walk-in, box-type 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 × 2 m wide × 2 m deep, with a door 2 m high × 1 m wide following the recommendations of Barber and Bildstein (2011). The second trap had dimensions of 2 m high × 3 m wide × 3 m deep, and a door of 2 m high × 1.3 m wide. The swing-doors were activated by a rope leading to a hide 30 m away to minimize disturbance. We used cow carcasses from the local slaughterhouse as bait.

We captured 10 individual vultures (King Vultures = 5; Greater Yellow-headed Vultures = 5), all of which were in adult plumage (> 3 years of age). 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 42 g, $n = 3$; Greater Yellow-headed Vulture tag size 27 g, $n = 5$), and two King Vulture individuals were fitted with Northstar (<https://www.northstarst.com>) Phoenix solar-panelled, 40-g GPS satellite tags which did not include altimeters and accelerometers. The tags were attached with Teflon thoracic (X-strap)

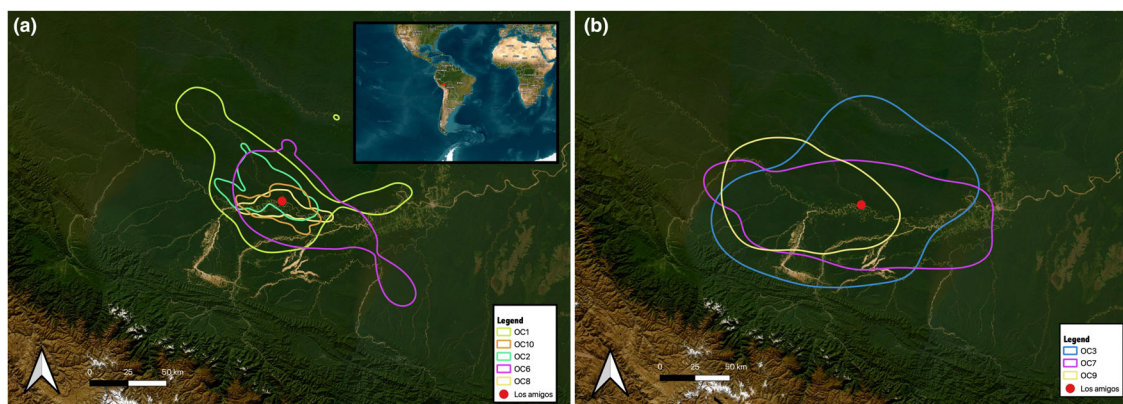


Figure 1. A map of the study site in the Peruvian Amazon with auto-correlated kernel density home-range estimators: red dot = Los Amigos Biological Station; coloured lines = individual 95% kernel density home-range estimates. (a) Greater Yellow-headed Vulture; (b) King Vulture.

harnesses (Wolter *et al.* 2018, Anderson *et al.* 2020, Bildstein *et al.* 2020). The e-obs tags were set to acquire locations every hour when battery levels were low and every 10 min when battery levels were high, from 05:00 to 19:00 h local time. The e-obs tags were fitted with GSM receivers, which uploaded data when passing cell-phone towers. Phoenix tags collected hourly locations 24 h a day with uplink via the Globalstar Satellite System. All movement data were stored on Movebank (Kays *et al.* 2022; and represent a subset of the individuals within the project 'OC Vultures').

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 (Kahn *et al.* 1998) *post-hoc*, which designated two males and three females of each species (Supporting Information Appendix A). We do not include sex as a covariate in our data analysis owing to low sample size. All precautions and necessary care were taken to reduce potential discomfort or harm to the birds. Vulture handling times were kept to a minimum to reduce stress; the average processing time (from capture to release) was 68 min (min = 30; max = 91). The weight of the transmitters and the method of fitting the devices followed standard protocols and recommendations; we ensured the total weight of the tag and the harness did not exceed 4% of the bodyweight of each individual

(Sergio *et al.* 2015) and created device fitting protocols from the following references (Diekmann *et al.* 2004, Barber & Bildstein 2011, Sergio *et al.* 2015, Wolter *et al.* 2018, Bildstein *et al.* 2020). A permit for equipping vultures with the GPS transmitters 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. As part of the permit approval process the SERFOR scientific committee evaluated the ethical implications of the proposed capture and device deployment methods and raised no issues.

Biometric measurements

We took a suite of morphometric data using standard measurements as described for vultures in Mundy and Butchart (1992). Here, we use data from two of these traits: (1) 'body mass', using digital precision scales to the nearest gram, and (2) 'wing span', representing the sum of the distance in centimetres from the midpoint between the shoulders to the tip of the longest primary feather on the left and right wings, with each wing laid out alternately on a flat surface. We also downloaded published measurements of two traits measured from museum specimens – 'culmen depth' and 'hang wing index' from the AVONET database (Tobias *et al.* 2022). Culmen depth ($n = 10$; Appendix C) is a trait shown to be important in discriminating the feeding habitats of vultures (Hertel 1994) and the hang wing index represents

the ratio between the distance between the tip of the first secondary feather and the tip of the longest primary to the total wing chord length ($n = 8$; Appendix C). A high wing index indicates a wing suitable for efficient long-distance flights, whereas a low index is associated with lower efficiency, shorter flights (Sheard *et al.* 2020).

Carcass arrival monitoring

To explore the temporal dynamics of carcass discovery and consumption by sympatric vulture species, we deployed six 50-kg pig carcasses in the area surrounding Los Amigos Biological Station between 7 September 2021 and 15 March 2022. Carcass locations were selected based on accessible forest within 50 m of the river banks. The area surrounding the carcasses was cleared of small vegetation in a 5-m radius from the centre point. Carcasses were monitored by two camera traps, one placed 2 m from the carcass and one 5 m from the carcass. Cameras were set to record a single image per motion trigger, with a quiet period of 10 min between successive triggers. Images were identified to species level manually in the Wildlife Insights camera trap management platform (Ahumada *et al.* 2020). 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): (1) 'arrival order' – defined as the order in which each vulture species was first detected at a given carcass; (2) 'arrival time in daylight hours' – defined as the number of daylight hours (06:00–18:00 h, as vultures do not typically fly at night) that elapse between carcass deployment and their first detection on a camera trap; and (3) 'proportion of detections' – defined as the proportion of images which contain each given species each hour.

Data analysis

Movement characteristics

The movement data analysed here were collected between 10 July 2021 and 31 October 2022, covering 156 704 locations. Six of the trackers functioned for the full survey duration, but four failed beforehand, giving a mean number of collection days per individual of 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 GPS error (we found none). Data were then filtered to remove segments with implausible speeds between successive fixes (> 100 kmph – the top reported speed for similar vulture species), resulting in the removal of a single data point.

Home-range. For all individuals with > 200 days of raw tracking data ($n = 8$), we calculated home-ranges using the Auto-correlated kernel density estimate (AKDE) function with default parameters within the 'ctmm' package (Calabrese *et al.* 2016, Fleming & Calabrese 2017). The AKDE estimator takes auto-correlated data and limited sample sizes into consideration, mitigating the issue of between-individual variation in sample size and sampling rate when using traditional KDE estimators (Silva *et al.* 2022). Variograms were constructed for each individual to verify 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 within the time period assessed). Various movement models (continuous-space and continuous-time stochastic movement models) were 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 generalized linear models using the 'lme4' package in R (Bates *et al.* 2014).

Daily movement characteristics. We calculated daily movement characteristics for all days where we had at least one recorded location before 08:00 h, and at least one location after 18:00 h, which represent the roosting locations, and at least one location recorded within all intermediate hours between the start and end times. We assumed that all locations with an instantaneous ground speed ≥ 4 m/s were 'flying', and < 4 m/s 'not flying' (see Appendix B). Using this dataset we estimated the following characteristics:

- 1 'number of flight bouts' – defined as the number of times a given individual transitions from not flying to flying each day;
- 2 'time of roost departure' – defined as the first recorded flight time in a given day minus the time interval between the first recorded flight time and the observation prior to it;
- 3 'time of roost arrival' – defined as the time of the last recorded flying location on a given day plus the time interval to the following non-flying location;
- 4 'total time in flight' – defined as the sum of the durations of each flight bout on a given day;
- 5 'total flight distance' – defined as the sum of all in-flight movement steps taken within a given day;
- 6 'daily roost displacement' – defined as the Euclidean distance between the start and end roost each day. All daily movement characteristics were compared using linear mixed effects model with individual ID as a random intercept term to account for repeated measurements using the 'lme4' package in R (Bates *et al.* 2014).

Flight bout characteristics. We subset the movement data into unique individual flights, and filtered this dataset to only include flights which lasted > 20 min, and which were recorded in high resolution for their entirety (< 15 min between successive locations). We used this dataset to estimate the following characteristics:

- 1 'flight duration' – defined as the time interval between the estimated start time (first flying observation minus the time interval to the observation prior to it) and the estimated end time (last flying observation plus the time interval to the subsequent non-flying observation);
- 2 'distance travelled' – defined as the sum of all movement steps within the flight bout;
- 3 'displacement distance' – defined as the Euclidean distance between the non-flying location before the flight bout starts and the first non-flying location after the flight bout has ended;
- 4 'straightness index' (following Fluhr *et al.* 2021) – defined as the ratio between the 'displacement distance' and 'distance travelled'.

All flight bout characteristics were compared using linear mixed effect models with individual

ID as a random intercept term to account for repeated measurements using the 'lme4' package in R (Bates *et al.* 2014).

Individual location characteristics. To characterize the movement characteristics at each unique location we subset the data to only include locations where individuals were flying (ground speed ≥ 4 m/s; see Appendix B; Péron *et al.* 2020) and tags which included ground speed and height information ($n = 8$). 'Ground speed' was reported in m/s. '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 to 2000 m, which resulted in the removal of three values which probably arose due to height estimation errors (see Appendix B). Both characteristics were compared using linear mixed effects model with individual ID as a random intercept term to account for repeated measurements using the 'lme4' package in R (Bates *et al.* 2014).

Biometric comparisons

We used linear models in base R with the trait of interest as the response terms (weight, wing span, beak depth and hang wing index) and species as the explanatory variable. Significant differences between the species were assessed using analysis of variance (ANOVA) using a 0.05 threshold.

Carcass arrival patterns

To explore temporal patterns in carcass visitation we created single species binomial mixed effects models using the 'lme4' package in R (Bates *et al.* 2014). The proportion of images of each given species detected per hour was the response term and daylight hours since carcass deployment were included as linear and quadratic terms.

Carcass deployment code was included 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 (no time term) based on adjusted AIC (AICc) and only presented the results from the best supported model.

RESULTS

Movement characteristics

The average home-range of the King Vulture was estimated to be five times larger than the Greater Yellow-headed Vulture home-range (2750 vs. 13 000 km²; Fig. 1; Appendix D). Marked differences in daily movement characteristics were also detected. There was strong statistical support for King Vultures making fewer unique flight bouts (1.6 vs. 2.9 bouts; Fig. 2a), departing later (10:28 vs. 09:08 h; Fig. 2b) and arriving earlier (13:58 vs. 14:26 h; Fig. 2c) to roost sites, and spending less time in flight per day (150 vs. 240 min; Fig. 2d) compared with Greater Yellow-headed Vultures. Although there was no statistical support for differences between King and Greater Yellow-headed Vultures in the average daily distance travelled (30.5 vs. 28.0 km; Fig. 2e) or daily roost displacement distance (12.0 vs. 9.3 km; Fig. 2f), raw data distributions revealed a bimodal pattern in King Vulture displacements. The proportion of days in which King Vultures travelled < 10 km (26%) or > 80 km (15%) was greater than that of Greater Yellow-headed Vultures (21% and 1%, respectively; Fig. 2e). King Vulture roost displacements were > 40 km for 7% of days, vs. just 1% for Greater Yellow-headed Vultures (Fig. 2f).

At the individual flight scale, there was strong statistical support for King Vulture flights being longer (80 vs. 59 min; Fig. 3a), travelling further (18 vs. 8 km; Fig. 3b) and displacing further (7.6 vs. 3.6 km; Fig. 3d) compared with Greater Yellow-headed Vultures. There was no statistical support for straighter, more direct flights in either species (straightness index of 0.6 vs. 0.55; Fig. 3e). There was also strong statistical support for King Vultures having 40% faster flight speeds (11.8 vs. 8.4 m/s; Fig. 3c) and average flight height 265% higher (404 vs. 111 m; Fig. 3f) compared with the Greater Yellow-headed Vulture.

Biometric comparisons

There was strong statistical support for King Vultures being ~ 2 kg heavier than Greater Yellow-headed Vultures (Fig. 4a), but they had similar wing spans (KV = 168 vs. GYV = 164 cm; Fig. 4b). Analysing data from the AVONET database revealed statistical support for King Vultures having greater beak depth than Greater Yellow-headed Vultures (30.6 vs. 17.3 mm, respectively), and statistical support for higher hand wing index values (37.6 vs. 16.5, respectively).

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 one (Turkey Vultures) was detected at two of the six (33%). Greater Yellow-headed Vultures were the first species to be detected at the animal carcass in three of six occasions (50%), and second in the remaining 50% of cases (Fig. 5a), with the shortest average time until detection (5.3 daylight hours). Black Vultures were first to be detected at two of six 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, arriving third at five of six 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 (fourth) 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 most abundant species in the first 10 daylight hours from carcass deployment, being 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 daylight hours), the relative abundance of Greater Yellow-headed Vultures again began to rise. Turkey Vultures were infrequently detected across all times.

DISCUSSION

Here we use a complementary set of approaches and technologies, including data from on-bird

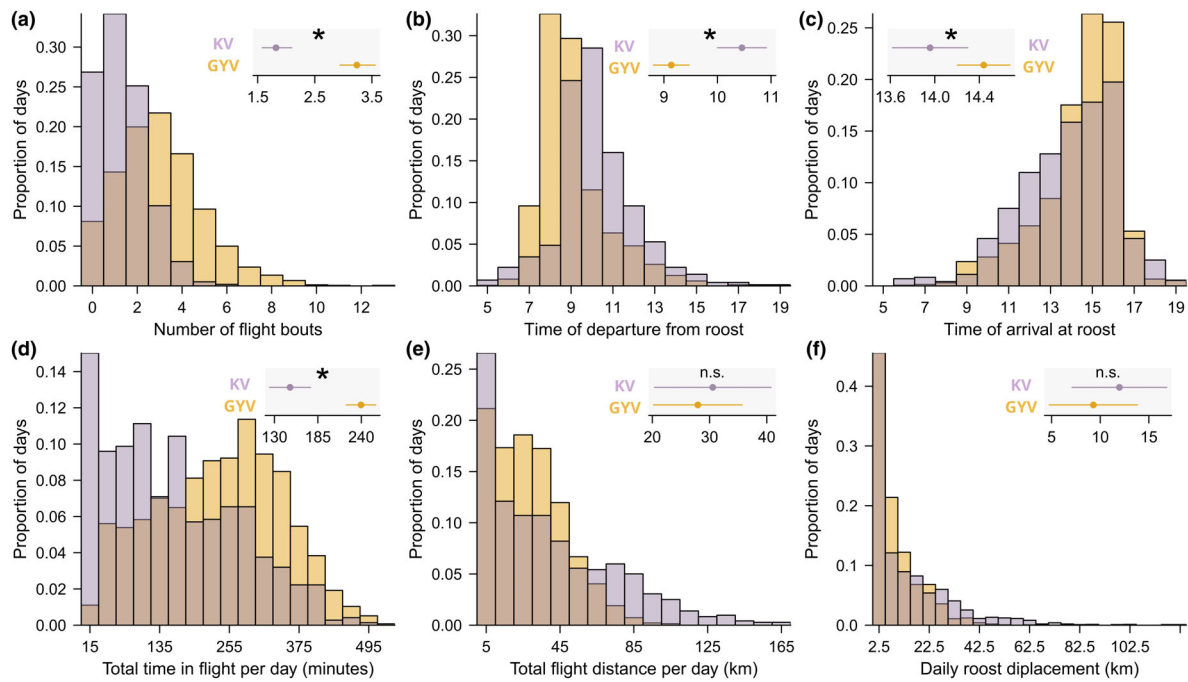


Figure 2. Daily movement characteristics of King Vultures (KV) and Greater Yellow-headed Vultures (GYV). (a) Number of flight bouts; (b) time of departure from night-time roost; (c) time of arrival at night-time roost; (d) total time in flight per day (min); (e) total flight distance per day (km); (f) daily roost displacement distance (km). Bar heights show the proportion of days in the dataset which take the given integer value (a–c) or binned range (d–e; histogram bin widths of 30 min, 10 km and 5 km, respectively). Inset panels show the model outputs with species-specific mean estimates (points), 95% confidence intervals (horizontal lines) and significant (*) or non-significant (n.s.) difference between species.

sensors, morphological measurements and camera trap-gathered carcass interaction data, to explore the foraging strategies of King and Greater Yellow-headed Vultures. We find marked differences in space use and flight characteristics related to foraging behaviour, and corresponding differences in carcass arrival times 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). We find a combination of movement characteristics and

morphological traits of Greater Yellow-headed Vultures consistent with them being ‘foraging scouts’ – they are relatively lightweight, depart the roost in the early morning, and fly relatively low over the forest canopy and across relatively small home-ranges. These traits, in combination with a well-developed sense of smell (Gomez *et al.* 1994), means that they are typically the first vulture species to ‘smell-out’ potential food sources and arrive at carcasses in closed-canopy forests. The King Vulture, in contrast, displays different movement characteristics – weighing over double that of a Greater Yellow-headed Vulture, they start flying later in the morning and have fewer flight bouts per day, perhaps reflecting a greater cost to get airborne. However, once flying, the King Vulture flies faster and higher and covers a substantially larger home-range than Greater Yellow-headed Vultures. These differences are consistent with hand wing index variation between the species (King Vultures have a larger index than Greater Yellow-headed Vultures), probably

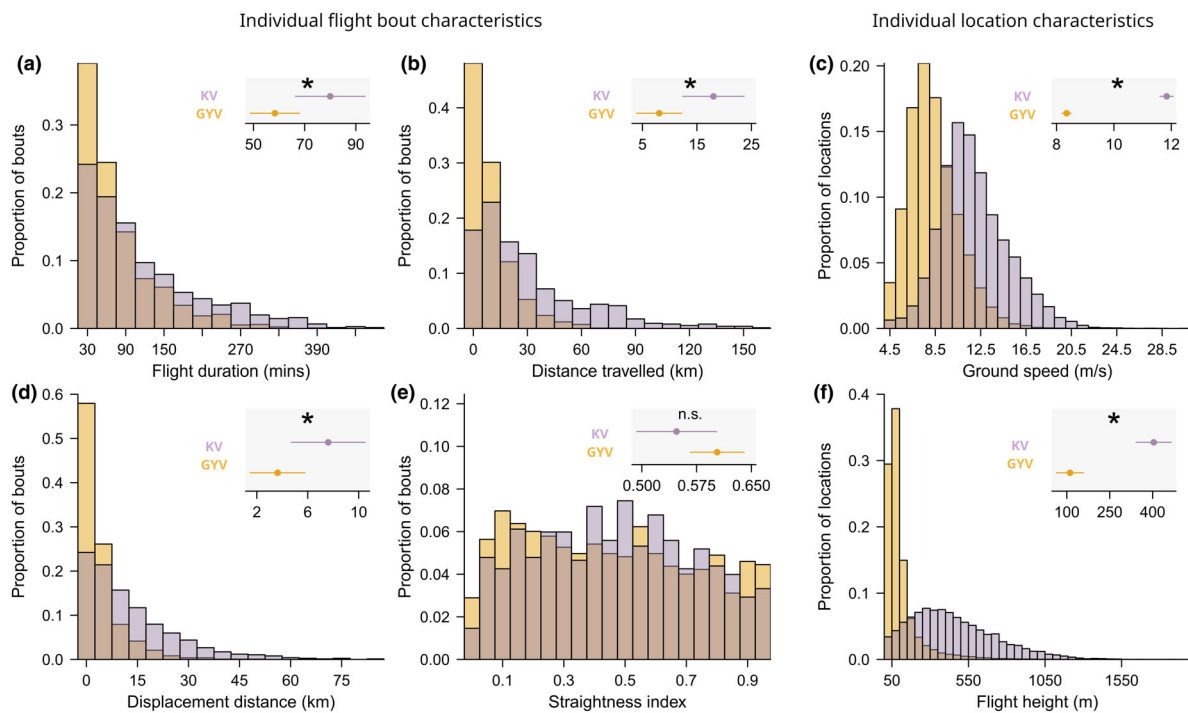


Figure 3. Flight bout and individual location characteristics of King Vultures (KV) and Greater Yellow-headed Vultures (GYV). (a) Flight duration (min); (b) distance travelled (km); (c) ground speed (m/s); (d) displacement distance (km); (e) straightness index; (f) flight height (m). Bar heights show the proportion of flights/locations in the dataset which take the binned range (a–f; histogram bin widths of 30 min, 10 km, 1 m/s, 5 km, 0.05 units and 50 m, respectively). Inset panels show the model outputs with species-specific mean estimates (points), 95% confidence intervals (horizontal lines), and significant (*) or non-significant (n.s.) difference between species.

reflecting either higher long-range flight efficiency in King Vultures, or Greater Yellow-headed Vultures being adapted to having greater manoeuvrability beneath the canopy.

The differences in morphological traits probably influence the flight/soaring ability of the focal species (Shepard & Lambertucci 2013): the low body mass of Greater Yellow-headed Vultures means they can probably exploit weaker thermal updrafts than King Vultures. The reduced cost of initiating flight is consistent with Greater Yellow-headed Vultures leaving the roost earlier and having more flight bouts per day than King Vultures. Interestingly, in African vultures the converse pattern appears – heavier species have greater carrion search efficiency than smaller species (e.g. Spiegel *et al.* 2013) – perhaps due to African vultures typically locating carrion visually and in more open environments than closed-canopy tropical rainforest. Given King Vultures' 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 probably rare. Indeed, other studies outside of the Neotropics have found that vultures tend to prefer carcasses not killed by predators (Kendall *et al.* 2012). Instead, they probably rely on signs of other birds as visual cues (also known as local enhancement; Cortés-Avizanda *et al.* 2014), e.g. the Greater Yellow-headed and Turkey Vultures, but most probably the large 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. These patterns are consistent with similar work from the Brazilian cerrado

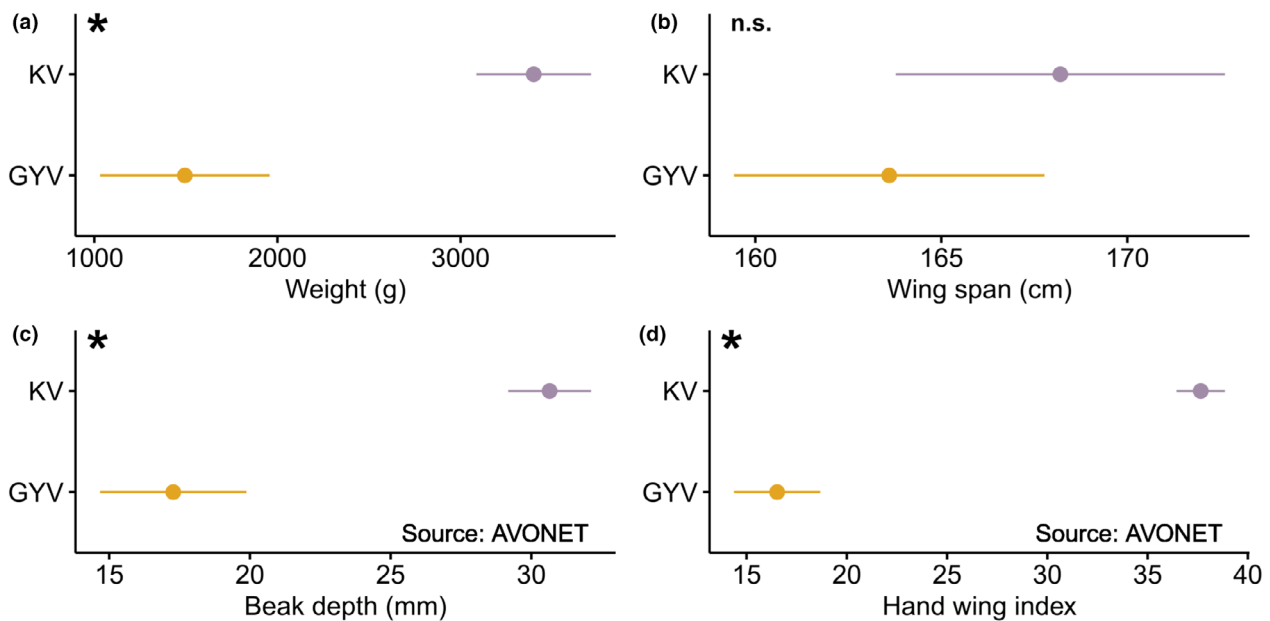


Figure 4. Error-bar plot of King Vulture (KV) and Greater Yellow-headed Vulture (GYV) morphometric measurements. (a) Weight (g); (b) wing span (cm); (c) beak depth (mm); (d) hand wing index. Points = species-specific mean values; vertical lines = 95% confidence intervals; * = significant difference between species; n.s. = no significant difference between species. Raw morphometric data are shown in Appendix C tables.

where the Cathartid vultures (Lesser Yellow-headed *Cathartes burrovianus* and Turkey) arrived earlier to carcasses compared with Black and King Vultures (Naves-Alegre *et al.* 2022a, 2022b).

Of the movement characteristics compared here, only three showed no statistical support for being different between the species: ‘daily roost displacement’, ‘total flight distance per day’ and the individual flight ‘straightness index’. This is particularly surprising given the marked interspecies variation in home-range size. However, although there was no statistical support for differences in the average roost displacement and total flight distances, the raw data showed that King Vultures have a greater proportion of days where they travel < 10 km (perhaps due to greater cost to get airborne), and a greater proportion of days where they travel > 80 km and displace their roost by > 40 km (perhaps due to higher relative flight efficiency and differing search tactics). This suggests that relatively rare long-distance displacements could drive the difference in home-range size, rather than fundamental differences in flight tortuosity between the species.

Consistent with the movement characteristics and trait data, we find no evidence of spatial niche

separation between King, Greater Yellow-headed and Black Vultures at provisioned carcasses – they were detected at all provisioning events. Instead, 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 Vultures did often remain in the vicinity of the carcass and, after 50 h, would become the dominant species at carcasses once again – suggesting that they can utilize older carrion or that they specialize in cleaning up remaining sinew and cartilage left by the King and Black Vultures. Notably the returning/remaining pattern of Greater Yellow-headed Vultures was not observed in the Lesser Yellow-headed Vulture in the Brazilian cerrado (Naves-Alegre *et al.* 2022a, 2022b), suggesting different foraging tactics between these sister species. These visitation differences are supported by variation in beak depth between the species: King Vultures have deep bills consistent with the ‘ripper’ feeding guild (which primarily feeds on skin and the carcass hide; Hertel 1994), whereas the relatively shallow-billed

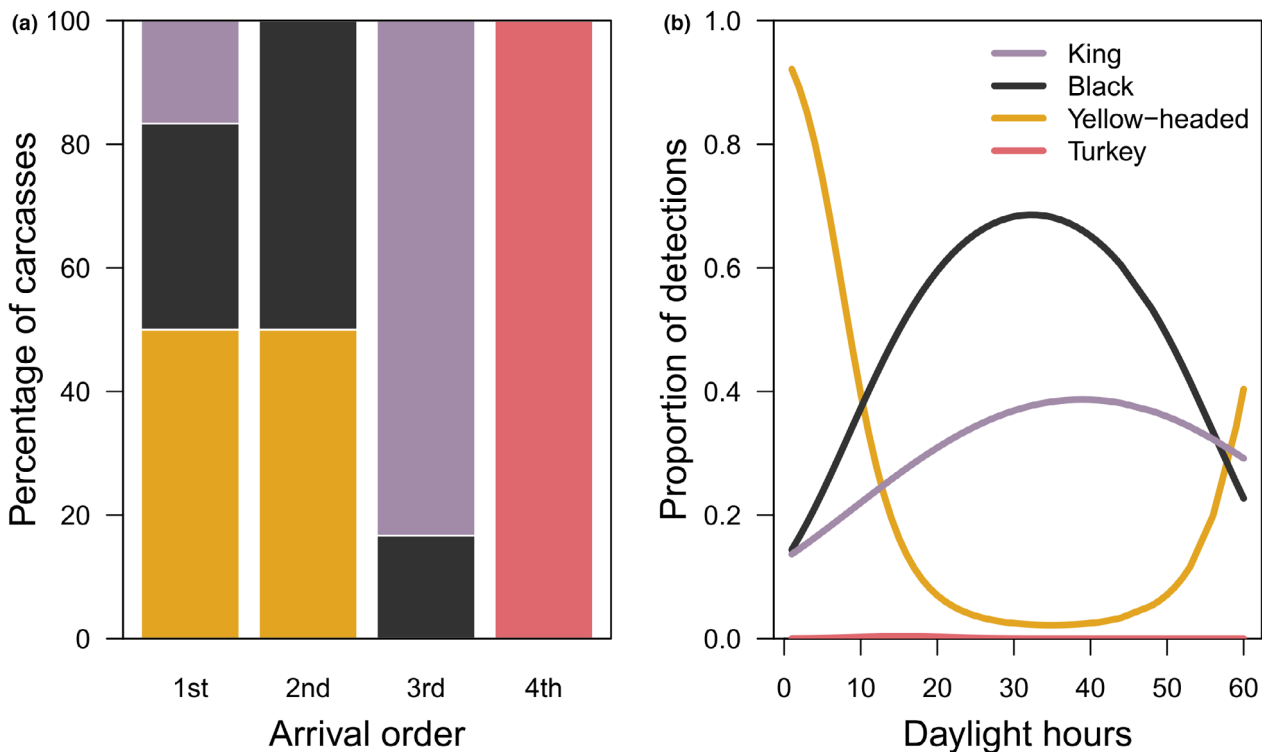


Figure 5. Arrival order ((a); the order at which species were detected at provisioned carcasses) and the predicted proportion of detections through time ((b); estimated proportion of detections of a given species in relation to the number of daylight hours since carcass deployment, from single-species mixed-effects model) for each of the vulture species detected.

Greater Yellow-headed Vulture belongs to the ‘scrapper’ guild (which feed on scraps around the carcass; Hertel 1994). Interestingly, the Turkey Vulture was only detected at one of the six carcasses, suggesting some element of spatial niche separation, a preference for very recently deceased carrion or a species which is in low relative abundance in this system. Previous work has shown that Turkey 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 (~ 50 kg) to mimic larger rainforest vertebrates, such as peccaries, tapir or capybara. However, it has been shown in the Brazilian cerrado (Naves-Alegre *et al.* 2022a, 2022b), African regions (Kendall *et al.* 2012) and Europe (Moreno-Opo *et al.* 2015, 2016) that different sized carcasses contribute to the resource partitioning of vultures. Perhaps smaller carcasses are

quickly discovered by Greater Yellow-headed or Turkey Vultures, which have the greatest sense of smell and ‘scouting’ ability, allowing them to 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 stratify between different habitat types to gain a more complete picture of the mechanisms promoting coexistence in Neotropical vulture communities.

Our movement and biometric data are limited by a relatively small sample size of birds. However, they

represent the first GPS-tagged individuals of King and Greater Yellow-headed Vultures to be published. Expanding the tracking and carcass provisioning initiatives to more individuals, throughout a broader set of habitats, seasons and in locations with and without sympatric species, would allow assessments of context-dependent foraging behaviours and linking intraspecific variation in morphological characteristics with flight and feeding 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, Harel *et al.* 2017, Williams & 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), and how variation in morphological traits is linked to variation in flight performance (Pennycuik 2008). 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 the species thought to depend on contiguous undisturbed habitats (e.g. Greater Yellow-headed or King Vulture) could ultimately lead to decreased diversity and homogenization of the scavenger community, 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.

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AUTHOR CONTRIBUTIONS

Christopher Beirne: Writing – original draft; writing – review and editing; investigation; methodology; visualization; software; formal analysis; data curation; supervision; project administration. **Mark Thomas:** Writing – original draft; writing – review and editing; investigation; data curation; formal analysis; visualization; methodology; software. **Arianna Basto:** Writing – review and editing; investigation; project administration; methodology; data curation; writing – original draft. **Eleanor Flatt:** Writing – review and editing; investigation; data curation; project administration; methodology; writing – original draft. **Giancarlo Inga Diaz:** Writing – review and editing; investigation; methodology; data curation. **Diego Rolim Chulla:** Writing – review and editing; investigation; methodology; data curation. **Flor Perez Mullisaca:** Writing – review and editing; investigation; methodology; data curation. **Rosio Vega Quispe:** Writing – review and editing; investigation; data curation; methodology. **Caleb Jonatan Quispe Quispe:** Writing – review and editing; investigation; methodology; data curation. **Adrian Forsyth:** Conceptualization; funding acquisition; writing – review and editing; supervision; resources. **Andrew Whitworth:** Conceptualization; funding acquisition; writing – review and editing; writing – original draft; investigation; supervision; project administration; resources; formal analysis; methodology.

ETHICS NOTE

This study involved the capture and handling of wild animals. To ensure the safety and welfare of both the wild animals and the field team, this research project followed already established protocols for large raptors (vultures). The capture

protocols were carried out by experienced and trained wildlife veterinarians and biologists to ensure the health and safety of the animals. An ethical assessment of the capture and device deployment protocols was performed by the SERFOR scientific committee as part of the permit process (No. AUT-IFS-2021-039, 18 June 2021). Personal protective equipment (PPE) was always utilized 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 bodyweight to ensure the bird is healthy post-capture and there are no factors reducing the survival of the bird.

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CONFLICT OF INTERESTS

The authors declare that no conflicts of interest exist.

Data Availability Statement

Movement/tracking datasets used in this study are openly available on Movebank (movebank.org, study name 'OC Vultures') and will be archived in the Movebank Data Repository with a citable DOI upon acceptance for publication. Additional datasets generated in support of the conclusions of this article are included within the article and its additional files. The datasets generated and/or analyzed during the current study are available in the Movebank Data Repository, <https://doi.org/10.5441/001/1.320> (Beirne et al., 2024).

REFERENCES

Ahumada, J.A., Fegraus, E., Birch, T., Flores, N., Kays, R., O'Brien, T.G., Palmer, J., Schuttler, S., Zhao, J.Y. & Jetz, W. 2020. Wildlife insights: a platform to maximize the

- potential of camera trap and other passive sensor wildlife data for the planet. *Environ. Conserv.* **47**: 1–6.
- Anderson, D., Arkumarev, V., Botha, A., Bildstein, K., Bowden, C., Davies, M., Duriez, O., Forbes, N., Godino, A., Green, R., Krueger, S., Lambertucci, S., Orr-Ewing, D., Parish, C., Parry-Jones, J. & Weston, E. 2020. A Practical Guide to Methods for Attaching Research Devices to Vultures and Condors. *Vulture News* **78a**: 1–72.
- Barber, D.R. & Bildstein, K.L. 2011. A lightweight portable, walk-in trap for catching vultures. *Vulture News* **60**: 22–25.
- Bates, D., Mächler, M., Bolker, B. & Walker, S. 2014. Fitting Linear Mixed-Effects Models using lme4. *J Stat Softw* **67**, 48.
- Beirne C., Thomas M., Basto A., Flatt E., Diaz G.I., Chulla D.R., Mullisaca F.P., Quispe R.V., Quispe C.J.Q., Forsyth A., Whitworth A. 2024. Data from: Scouts vs usurpers: alternative foraging strategies facilitate coexistence between Neotropical cathartid vultures. Movebank Data Repository. <https://doi.org/10.5441/001/1.320>
- Bildstein, K., Botha, A. & Lambertucci, S.A. 2020. Thoracic X-strap harness. Design and method 1. *Vulture News* **78**: 18–26.
- Böhmer, C., PrevotEAU, J., Duriez, O. & Abourachid, A. 2020. Gulper, ripper and scrapper: anatomy of the neck in three species of vultures. *J. Anat.* **236**: 701–723.
- Buckley, N.J. 1997. Experimental tests of the information-center hypothesis with black vultures (*Coragyps atratus*) and Turkey vultures (*Cathartes aura*). *Behav. Ecol. Sociobiol.* **41**: 267–279.
- Calabrese, J.M., Fleming, C.H. & Gurarie, E. 2016. Ctrmm: an r package for analyzing animal relocation data as a continuous-time stochastic process. *Methods Ecol. Evol.* **7**: 1124–1132.
- Carrete, M., Lambertucci, S.A., Speziale, K., Ceballos, O., Travani, A., Delibes, M., Hiraldo, F. & Donazar, J.A. 2010. Winners and losers in human-made habitats: interspecific competition outcomes in two neotropical vultures: interspecific competition between neotropical vultures. *Anim. Conserv.* **13**: 390–398.
- Carucci, T., Whitehouse-Tedd, K., Yarnell, R.W., Collins, A., Fitzpatrick, F., Botha, A. & Santangeli, A. 2022. Ecosystem services and disservices associated with vultures: a systematic review and evidence assessment. *Ecosyst. Serv.* **56**: 101447.
- Cortés-Avizanda, A., Jovani, R., Carrete, M. & Donazar, J.A. 2012. Resource unpredictability promotes species diversity and coexistence in an avian scavenger guild: a field experiment. *Ecology* **93**: 2570–2579.
- Cortés-Avizanda, A., Jovani, R., Donazar, J.A. & Grimm, V. 2014. Bird sky networks: how do avian scavengers use social information to find carrion? *Ecology* **95**: 1799–1808.
- Costa-Pereira, R., Moll, R.J., Jesmer, B.R. & Jetz, W. 2022. Animal tracking moves community ecology: opportunities and challenges. *J. Anim. Ecol.* **91**: 1334–1344.
- Craig, C.A., Thomson, R.L. & Santangeli, A. 2018. Communal farmers of Namibia appreciate vultures and the ecosystem services they provide. *Ostrich* **89**: 211–220.
- Diekmann, M., Scott, A., Scott, M. & Diekmann, J. 2004. Capture and fitting of satellite-and radio-telemetry equipment onto Cape griffon vulture, *Gyps coprotheres*, African white-backed vulture *Gyps africanus* and lappet-faced

- vulture *Torgos tracheliotos* in the Waterberg area, Namibia in 2004. *Vulture News* 51: 34–45.
- Fleming, C.H. & Calabrese, J.M.** 2017. A new kernel density estimator for accurate home-range and species-range area estimation. *Methods Ecol. Evol.* 8: 571–579.
- Fluhr, J., Peyrusque, D., Duriez, O. & Benhamou, S.** 2021. Space use and time budget in two populations of griffon vultures in contrasting landscapes. *J. Raptor Res.* 55: 425–437.
- Gangoso, L., Agudo, R., Anadón, J.D., de la Riva, M., Suleyman, A.S., Porter, R. & Donazar, J.A.** 2013. Reinventing mutualism between humans and wild fauna: insights from vultures as ecosystem services providers: reinventing human-vulture mutualism. *Conserv. Lett.* 6: 172–179.
- Gomez, L.G., Houston, D.C., Cotton, P. & Tye, A.** 1994. The role of greater yellow-headed vultures *Cathartes melambrotus* as scavengers in neotropical forest. *Ibis* 136: 193–196.
- Grigg, N.P., Krilow, J.M., Gutierrez-Ibanez, C., Wylie, D.R., Graves, G.R. & Iwaniuk, A.N.** 2017. Anatomical evidence for scent guided foraging in the Turkey vulture. *Sci. Rep.* 7: 17408.
- Harel, R., Spiegel, O., Getz, W.M. & Nathan, R.** 2017. Social foraging and individual consistency in following behaviour: testing the information centre hypothesis in free-ranging vultures. *Proc. R. Soc. B Biol. Sci.* 284: 20162654.
- van den Heever, L., Thompson, L.J., Bowerman, W.W., Smit-Robinson, H., Shaffer, L.J., Harrell, R.M. & Ottinger, M.A.** 2021. Reviewing the role of vultures at the human-wildlife-livestock disease interface: an African perspective. *J. Raptor Res.* 55: 311–327.
- Hertel, F.** 1994. Diversity in body size and feeding morphology within past and present vulture assemblages. *Ecology* 75: 1074–1084.
- Holland, A.E., Byrne, M.E., Bryan, A.L., DeVault, T.L., Rhodes, O.E. & Beasley, J.C.** 2017. Fine-scale assessment of home-ranges and activity patterns for resident black vultures (*Coragyps atratus*) and turkey vultures (*Cathartes aura*). *PLoS One* 12: e0179819.
- Holland, A.E., Byrne, M.E., Hepinstall-Cymerman, J., Bryan, A.L., DeVault, T.L., Rhodes, O.E. & Beasley, J.C.** 2019. Evidence of niche differentiation for two sympatric vulture species in the southeastern United States. *Mov. Ecol.* 7: 31.
- Houston, D.C.** 1984. Does the king vulture *Sarcorhamphus papa* use a sense of smell to locate food? *Ibis* 126: 67–69.
- Houston, D.C.** 1986. Scavenging efficiency of turkey vultures in tropical forest. *Condor* 88: 318–323.
- IUCN.** 2023. *Sarcorhamphus papa*: BirdLife International: The IUCN Red List of Threatened Species <https://www.iucnredlist.org>. Accessed January 2024
- Jackson, A.L., Ruxton, G.D. & Houston, D.C.** 2008. The effect of social facilitation on foraging success in vultures: a modelling study. *Biol. Lett.* 4: 311–313.
- Jeltsch, F., Bonte, D., Pe'er, G., Reineking, B., Leimgruber, P., Balkenhol, N., Schröder, B., Buchmann, C.M., Mueller, T., Blaum, N., Zurell, D., Böhning-Gaese, K., Wiegand, T., Eccard, J.A., Hofer, H., Reeg, J., Eggers, U. & Bauer, S.** 2013. Integrating movement ecology with biodiversity research - exploring new avenues to address spatiotemporal biodiversity dynamics. *Mov. Ecol.* 1: 6.
- Kahn, N.W., St. John, J. & Quinn, T.W.** 1998. Chromosome-specific intron size differences in the avian CHD gene provide an efficient method for sex identification in birds. *Auk* 115: 1074–1078.
- Kays, R., Davidson, S.C., Berger, M., Bohrer, G., Fiedler, W., Flack, A., Hirt, J., Hahn, C., Gauggel, D., Russell, B., Kölzsch, A., Lohr, A., Partecke, J., Quetting, M., Safi, K., Scharf, A., Schneider, G., Lang, I., Schaeuffelhut, F., Landwehr, M., Storhas, M., Van Schalkwyk, L., Vinciguerra, C., Weinzierl, R. & Wikelski, M.** 2022. The Movebank system for studying global animal movement and demography. *Methods Ecol. Evol.* 13: 419–431.
- Kendall, C.J.** 2014. The early bird gets the carcass: temporal segregation and its effects on foraging success in avian scavengers. *Auk Ornithol. Adv.* 131: 12–19.
- Kendall, C., Virani, M.Z., Kirui, P., Thomsett, S. & Githiru, M.** 2012. Mechanisms of coexistence in vultures: understanding the patterns of vulture abundance at carcasses in Masai Mara National Reserve, Kenya. *Condor* 114: 523–531.
- Long, J.A.** 2015. Quantifying spatial-temporal interactions from wildlife tracking data: issues of space, time, and statistical significance. *Procedia Environ. Sci.* 26: 3–10.
- Lovejoy, T.E. & Nobre, C.** 2019. Amazon tipping point: last chance for action. *Sci. Adv.* 5: eaba2949.
- Mateo-Tomás, P., Olea, P.P., Selva, N. & Sánchez-Zapata, J.A.** 2019. Species and individual replacements contribute more than nestedness to shape vertebrate scavenger metacommunities. *Ecography* 42: 365–375.
- McClure, C.J., Westrip, J.R., Johnson, J.A., Schulwitz, S.E., Virani, M.Z., Davies, R., Symes, A., Wheatley, H., Thorstrom, R. & Amar, A.** 2018. State of the world's raptors: distributions, threats, and conservation recommendations. *Biol. Conserv.* 227: 390–402.
- Moreno-Opo, R., Trujillano, A., Arredondo, Á., González, L.M. & Margalida, A.** 2015. Manipulating size, amount and appearance of food inputs to optimize supplementary feeding programs for European vultures. *Biol. Conserv.* 181: 27–35.
- Moreno-Opo, R., Trujillano, A. & Margalida, A.** 2016. Behavioral coexistence and feeding efficiency drive niche partitioning in European avian scavengers. *Behav. Ecol.* 27: 1041–1052.
- Moreno-Opo, R., Trujillano, A. & Margalida, A.** 2020. Larger size and older age confer competitive advantage: dominance hierarchy within European vulture guild. *Sci. Rep.* 10: 2430.
- Mundy, P.J. & Butchart, D.** 1992. *The vultures of Africa*. Randburg and Halfway House. Available at: <https://cir.nii.ac.jp/crid/1130282272364798336>. (accessed 15 January 2023)
- Nathan, R., Monk, C.T., Arlinghaus, R., Adam, T., Alós, J., Assaf, M., Baktoft, H., Beardsworth, C.E., Bertram, M.G., Bijleveld, A.I., Brodin, T., Brooks, J.L., Campos-Candela, A., Cooke, S.J., Gjelland, K.Ø., Gupte, P.R., Harel, R., Hellström, G., Jeltsch, F., Killen, S.S., Klefoth, T., Langrock, R., Lennox, R.J., Lourie, E., Madden, J.R., Orchan, Y., Pauwels, I.S., Riha, M., Roeleke, M., Schlägel, U.E., Shohami, D., Signer, J., Toledo, S., Vilck, O., Westrelin, S., Whiteside, M.A. & Jarić, I.** 2022. Big-data approaches lead to an increased understanding of the ecology of animal movement. *Science* 375: eabg1780.

- Naves-Alegre, L., Morales-Reyes, Z., Sánchez-Zapata, J.A. & Sebastián-González, E. 2022a. Scavenger assemblages are structured by complex competition and facilitation processes among vultures. *J. Zool.* **318**: 260–271.
- Naves-Alegre, L., Morales-Reyes, Z., Sánchez-Zapata, J.A., Sebastián-González, E. & Ovaskainen, O. 2022b. Scavenging in the realm of senses: smell and vision drive recruitment at carcasses in neotropical ecosystems. *Proc. R. Soc. B Biol. Sci.* **289**: 20220843.
- Ogada, D.L., Keesing, F. & Virani, M.Z. 2012. Dropping dead: causes and consequences of vulture population declines worldwide. *Ann. N. Y. Acad. Sci.* **1249**: 57–71.
- Olea, P.P., Iglesias, N. & Mateo-Tomás, P. 2022. Temporal resource partitioning mediates vertebrate coexistence at carcasses: the role of competitive and facilitative interactions. *Basic Appl. Ecol.* **60**: 63–75.
- Pain, D.J., Bowden, C.G.R., Cunningham, A.A., Cuthbert, R., Das, D., Gilbert, M., Jakati, R.D., Jhala, Y., Khan, A.A., Naidoo, V., Oaks, J.L., Parry-Jones, J., Prakash, V., Rahmani, A., Ranade, S.P., Baral, H.S., Senacha, K.R., Saravanan, S., Shah, N., Swan, G., Swarup, D., Taggart, M.A., Watson, R.T., Virani, M.Z., Wolter, K. & Green, R.E. 2008. The race to prevent the extinction of South Asian vultures. *Bird Conserv. Int.* **18**: S30–S48.
- Pavlis, N.K., Holmes, S.A., Kenyon, S.C. & Factor, J.K. 2012. The development and evaluation of the earth gravitational model 2008 (EGM2008). *J. Geophys. Res. Solid Earth* **117**: 1–38.
- Pennycook, C.J. 2008. *Modelling the Flying Bird*. London: Elsevier.
- Péron, G., Calabrese, J.M., Duriez, O., Fleming, C.H., García-Jiménez, R., Johnston, A., Lambertucci, S.A., Safi, K. & Shepard, E.L.C. 2020. The challenges of estimating the distribution of flight heights from telemetry or altimetry data. *Anim. Biotelemetry* **8**: 5.
- Poessel, S.A., Duerr, A.E., Hall, J.C., Braham, M.A. & Katzner, T.E. 2018. Improving estimation of flight altitude in wildlife telemetry studies. *J. Appl. Ecol.* **55**: 2064–2070.
- Rabenold, P.P. 1987. Recruitment to food in black vultures: evidence for following from communal roosts. *Anim. Behav.* **35**: 1775–1785.
- Santangeli, A., Buechley, E.R., Mammola, S. & Lambertucci, S.A. 2022. Priorities for research and action to prevent a New World vulture crisis. *Biol. Conserv.* **270**: 109563.
- Schlee, M.A. 2007. King vultures (*Sarcoramphus papa*) follow jaguar in the Serranía de la Cerbatana, Venezuela. *Vulture News* **57**: 4–16.
- Sebastián-González, E., Barbosa, J.M., Pérez-García, J.M., Morales-Reyes, Z., Botella, F., Olea, P.P., Mateo-Tomás, P., Moleón, M., Hiraldo, F., Arrondo, E., Donázar, J.A., Cortés-Avizanda, A., Selva, N., Lambertucci, S.A., Bhattacharjee, A., Brewer, A., Anadón, J.D., Abernethy, E., Rhodes, O.E. Jr., Turner, K., Beasley, J.C., DeVault, T.L., Ordiz, A., Wikenros, C., Zimmermann, B., Wabakken, P., Wilmers, C.C., Smith, J.A., Kendall, C.J., Ogada, D., Buechley, E.R., Frehner, E., Allen, M.L., Wittmer, H.U., Butler, J.R.A., du Toit, J.T., Read, J., Wilson, D., Jerina, K., Krofel, M., Kostecke, R., Inger, R., Samson, A., Naves-Alegre, L. & Sánchez-Zapata, J.A. 2019. Scavenging in the Anthropocene: human impact drives vertebrate scavenger species richness at a global scale. *Glob. Chang. Biol.* **25**: 3005–3017.
- Selva, N. & Fortuna, M.A. 2007. The nested structure of a scavenger community. *Proc. R. Soc. B Biol. Sci.* **274**: 1101–1108.
- Sergio, F., Tavecchia, G., Tanferna, A., López Jiménez, L., Blas, J., De Stephanis, R., Marchant, T.A., Kumar, N. & Hiraldo, F. 2015. No effect of satellite tagging on survival, recruitment, longevity, productivity and social dominance of a raptor, and the provisioning and condition of its offspring. *J. Appl. Ecol.* **52**: 1665–1675.
- Sheard, C., Neate-Clegg, M.H.C., Alioravainen, N., Jones, S.E.I., Vincent, C., MacGregor, H.E.A., Bregman, T.P., Claramunt, S. & Tobias, J.A. 2020. Ecological drivers of global gradients in avian dispersal inferred from wing morphology. *Nat. Commun.* **11**: 2463.
- Shepard, E.L.C. & Lambertucci, S.A. 2013. From daily movements to population distributions: weather affects competitive ability in a guild of soaring birds. *J. R. Soc. Interface* **10**: 20130612.
- Silva, I., Fleming, C.H., Noonan, M.J., Alston, J., Folta, C., Fagan, W.F. & Calabrese, J.M. 2022. Autocorrelation-informed home-range estimation: a review and practical guide. *Methods Ecol. Evol.* **13**: 534–544.
- Spiegel, O., Getz, W.M. & Nathan, R. 2013. Factors influencing foraging search efficiency: why do scarce lappet-faced vultures outperform ubiquitous white-backed vultures? *Am. Nat.* **181**: E102–E115.
- Tobias, J.A., Sheard, C., Pigot, A.L., Devenish, A.J.M., Yang, J., Sayol, F., Neate-Clegg, M.H.C., Alioravainen, N., Weeks, T.L., Barber, R.A., Walkden, P.A., MacGregor, H.E.A., Jones, S.E.I., Vincent, C., Phillips, A.G., Marples, N.M., Montaña-Centellas, F.A., Leandro-Silva, V., Claramunt, S., Darski, B., Freeman, B.G., Bregman, T.P., Cooney, C.R., Hughes, E.C., Capp, E.J.R., Varley, Z.K., Friedman, N.R., Korntheuer, H., Corrales-Vargas, A., Trisos, C.H., Weeks, B.C., Hanz, D.M., Töpfer, T., Bravo, G.A., Remeš, V., Nowak, L., Carneiro, L.S., Moncada R., A.J., Matysioková, B., Baldassarre, D.T., Martínez-Salinas, A., Wolfe, J.D., Chapman, P.M., Daly, B.G., Sorensen, M.C., Neu, A., Ford, M.A., Mayhew, R.J., Fabio Silveira, L., Kelly, J.A., Annorbah, N.N.D., Pollock, H.S., Grabowska-Zhang, A.M., McEntee, J.P., Carlos T. Gonzalez, J., Meneses, C.G., Muñoz, M.C., Powell, L.L., Jamie, G.A., Matthews, T.J., Johnson, O., Brito, G.R.R., Zyskowski, K., Crates, R., Harvey, M.G., Jurado Zevallos, M., Hosner, P.A., Bradfer-Lawrence, T., Maley, J.M., Stiles, F.G., Lima, H.S., Provost, K.L., Chibesa, M., Mashao, M., Howard, J.T., Mlamba, E., Chua, M.A.H., Li, B., Gómez, M.I., García, N.C., Päckert, M., Fuchs, J., Ali, J.R., Derryberry, E.P., Carlson, M.L., Urriza, R.C., Brzeski, K.E., Prawiradilaga, D.M., Rayner, M.J., Miller, E.T., Bowie, R.C.K., Lafontaine, R.-M., Scofield, R.P., Lou, Y., Somarathna, L., Lepage, D., Illif, M., Neuschulz, E.L., Templin, M., Dehling, D.M., Cooper, J.C., Pauwels, O.S.G., Analuddin, K., Fjeldså, J., Seddon, N., Sweet, P.R., DeClerck, F.A.J., Naka, L.N., Brawn, J.D., Aleixo, A., Böhning-Gaese, K., Rahbek, C., Fritz, S.A., Thomas, G.H. & Schlegel, M. 2022. AVONET: morphological, ecological and geographical data for all birds. *Ecol. Lett.* **25**: 581–597.

- Williams, H.J. & Safi, K.** 2021. Certainty and integration of options in animal movement. *Trends Ecol. Evol.* **36**: 990–999.
- Wolter, K., Neser, W. & Hirschauer, M.T.** 2018. *Protocols for Mass Capturing, Handling, and Fitting Tracking Devices and Patagial (Wing) Tags on Vultures*. Scheerpoort: VulPro NPC.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Appendix S1. Appendices A–D referred to in the main text.