Cambodian vultures are now conservation dependent: an update on vulture populations in Cambodia

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មូលន័យសង្ខេប

អត្ថបទនេះរាយការណ៍អំពីទំហំ និងការប្រែប្រួលប៉ូពុយឡាស្យុង នៃសត្វត្មាតបីប្រភេទដែលមានទីជម្រកនៅក្នុងប្រទេសកម្ពុជា (ត្មាតភ្លើង ត្មាតត្នោត និងត្មាតផេះ) និងវាយតម្លៃពីប្រសិទ្ធភាពនៃកិច្ចខិតខំប្រឹងប្រែងអភិរក្សដែលបានកំពុងអនុវត្ត។ ទិន្នន័យចំនួនប៉ូពុយឡាស្យុងសត្វត្មាតដែលយើងបង្ហាញត្រូវបានប្រមូលក្នុងអំឡុងពេលធ្វើជំរឿនដំណាលគ្នានៅបួនទីតាំងចាប់ពីខែមីនា ឆ្នាំ2014 រហូតដល់ខែធ្នូ ឆ្នាំ2024 និងការរាប់ជាប្រចាំនៅកន្លែងផ្តល់ចំណីរយៈពេលវែងចាប់ពីខែកក្កដា ឆ្នាំ2016 ដល់ខែធ្នូ ឆ្នាំ2024។ លទ្ធផលរបស់យើងបង្ហាញថា ចំនួនប៉ូពុយឡាស្យុងមានស្ថេរភាពនៃសត្វត្មាតត្នោត 78 ក្បាល និងសត្វត្មាតផេះមាន 48 ក្បាល នៅក្នុងឆ្នាំ2024 ជាមួយការសិក្សាពីមុនបង្ហាញថាចំនួនសត្វត្មាតពីរប្រភេទនេះមានការកើនឡើងនាប៉ុន្មានឆ្នាំថ្មីៗនេះនៅប្រទេសកម្ពុជា។ ទោះជាយ៉ាងណាក៏ដោយ សត្វត្មាតភ្លើងនៅតែមានចំនួនធ្លាក់ចុះទូទាំងប្រទេសដែលមានចំនួនត្រឹមតែ 14 ក្បាល ប៉ុណ្ណោះនៅឆ្នាំ2024។ ការផ្តល់ចំណីបន្ថែមមានប្រសិទ្ធភាពក្នុងការកាត់បន្ថយផលប៉ះពាល់នៃការពុលគគ្នា (secondary poisoning) និងកង្វះចំណីក្នុងធម្មជាតិ តែយ៉ាងណាក្តី ការហើរមកជុំគ្នានៃសត្វត្មាតនៅជុំវិញកន្លែងផ្តល់ចំណីក៏អាចបង្កើនភាពងាយរងគ្រោះរបស់ពួកវាទៅនឹងព្រឹត្តិការណ៍ពុលដ៏មហន្តរាយផងដែរ។ យើងសន្និដ្ឋានថា ចំនួនប៉ូពុយឡាស្យុងសត្វត្មាតនៅប្រទេសកម្ពុជាភាគច្រើនត្រូវបានគាំទ្រដោយការផ្តល់ចំណីបន្ថែមជាបន្តបន្ទាប់ ជាពិសេសនៅក្នុងដែនជម្រកសត្វព្រៃសៀមប៉ាង និងដែនជម្រកសត្វព្រៃឆែបព្រះរកា។ ចំនួនប៉ូពុយឡាស្យុងសត្វត្មាតនឹងធ្លាក់ចុះ និងប្រហែលជាអាចផុតពូជ បើគ្មានការផ្តល់សាកសពជាចំណីនៅកន្លែងទាំងនេះជាទៀងទាត់។ ដូច្នេះហើយ សត្វត្មាតនៅប្រទេសកម្ពុជា នាពេលបច្ចុប្បន្ននេះពឹងផ្អែកលើកម្មវិធីអភិរក្សដែលមានការចំណាយខ្ពស់ និងការគាំទ្រពីម្ចាស់ជំនួយពីខាងក្រៅដែលបន្ថែមភាពមិនច្បាស់លាស់ដល់និរន្តរភាពយូរអង្វែងនៃកិច្ចខិតខំប្រឹងប្រែងអភិរក្សនាពេលបច្ចុប្បន្ននេះ។

Abstract

This article reports the population sizes and trends of the three vulture species resident in Cambodia (red-headed vulture, slender-billed vulture and white-rumped vulture) and assesses the effectiveness of ongoing conservation efforts. The population data we present were collected during simultaneous census counts at four sites from March 2014 to December 2024 and regular counts at long-term feeding sites from July 2016 to December 2024. Our results indicate that populations of white-rumped and slender-billed vultures in Cambodia have stabilized (with 78 and 48

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birds counted in 2024, respectively), with the former even increasing in recent years. However, red-headed vultures are still declining nationally, with only 14 birds counted in 2024. Supplementary feeding has been effective in mitigating the impacts of secondary poisoning and natural food scarcity, although the resultant clustering of vultures around feeding sites increases their vulnerability to catastrophic poisoning events. We conclude that vulture populations in Cambodia are mostly supported by ongoing supplementary feeding, especially at Siem Pang Wildlife Sanctuary and Chhaeb-Preah Roka Wildlife Sanctuary. Populations would decline without regular provision of carcasses at these sites, probably to extinction. As such, vultures in Cambodia are now dependent on high-cost programmes and external donor support, which adds uncertainty to the long-term sustainability of current conservation efforts.

Keywords population, red-headed vulture, restaurant, slender-billed vulture, white-rumped vulture, wildlife sanctuary

Introduction

Scavenging, or the consumption of carrion, is a common foraging strategy among vertebrates and a critical component of ecosystem ecology (DeVault *et al*., 2016). In a functioning ecosystem, large numbers of animals can die from causes other than predation such as diseases, bacterial and parasitic infections, malnutrition or extreme climatic events (Olea *et al*., 2019; DeVault *et al*., 2003). Scavengers provide several ecosystem services to humans by disposing of carcasses (Moleón *et al*., 2014), particularly in terms of infectious disease and animal pest control (Ogada *et al*., 2012). Scavenging is widespread across the animal kingdom in terrestrial and aquatic ecosystems and almost all predator species feed on carrion to some extent (Selva *et al*., 2019). The unpredictable and ephemeral nature of carrion, and its temporal and geographical patchiness, has limited the evolution of true specialists on this resource.

Among vertebrates, only 22 species of birds, namely vultures, have evolved as obligate scavengers that rely solely on carrion for their survival and reproduction (Ruxton & Houston, 2004; DeVault *et al*., 2016; Kane *et al*., 2017; Selva *et al*., 2019). This particular trait makes them dependent on the spatial and temporal availability of carcasses, and extremely sensitive to the risks of contamination (Ruxton & Houston, 2004; Ogada *et al*., 2019). Seven of these species are resident in South Asia, most of which are listed as Critically Endangered or Endangered on the IUCN Red List of Threatened Species. These species are at high risk of extinction partly because their populations collapsed spectacularly in the 1990s and 2000s due to veterinary use of the non-steroidal anti-inflammatory drug diclofenac (Oaks *et al*., 2004). The toxicity of diclofenac when ingested by vultures through contaminated carrion is such that it is estimated that the global population of white-rumped vultures *Gyps bengalensis* crashed by over 99% in the last 30 years during the so-called South Asian vulture crisis, whereas populations of slender-billed vultures *Gyps tenuirostris* declined by nearly 97% and red-headed vultures *Sarcogyps calvus* by approximately 91% (Cuthbert *et al*., 2006; Prakash *et al*., 2007; BirdLife International, 2024).

In contrast, populations of these three species declined much earlier and for different reasons in Southeast Asia (Pain *et al*., 2003; Ogada *et al*., 2012). The three species were historically widespread and bred commonly in the first half of the 20th century, ranging from Myanmar across Thailand and Indochina, reaching Yunnan province in China and extending southwards to Peninsular Malaysia (Pain *et al*., 2003). During the second half of the century, political instability limited the collection of survey data in Indochina, leaving a gap in data on population trends. Notwithstanding this, historical declines of vultures are likely attributable to a decrease in carrion availability and changes in livestock husbandry practices. Loss of habitats in lowland plains and deciduous forests, their conversion to agriculture coupled with overhunting led to drastic declines in the once abundant populations of large wild ungulates that vulture populations depend for food, such as gaur *Bos gaurus*, banteng *B. javanicus* and water buffalo *Bubalus arnee* (Hla *et al*., 2011; Ogada *et al*., 2012).

With vulture populations in Myanmar and Cambodia now at historically low levels, human persecution, nest disturbance and accidental poisoning, once secondary threats, now appear to be the most immediate threats to the remaining birds (Hla *et al*., 2011; Clements *et al*., 2013; Loveridge *et al*., 2018). Since 2004, vulture populations in Cambodia have been monitored via national censuses undertaken by several governmental and non-governmental organisations. This led to research papers evaluating data collected in 2004–2011 (Clements *et al*., 2013) and 2011–2018 (Loveridge *et al*., 2018). Clements *et al*. (2013) examined the nesting success, ranging behaviour, population trends and threats to vultures in Cambodia. Their results indicate at least 296 vultures occurred

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within the country in 2010 (comprising 201 white-rumped vultures, 48 slender-billed vultures & 47 red-headed vultures) and pointed to secondary poisoning as the main cause of mortality in the country (73% of cases). While the exact compounds involved could not be identified, the authors suspected that organophosphates commonly used in agriculture were responsible, because extensive surveys indicated that use of diclofenac was uncommon in Cambodia (Clements *et al*., 2013).

Following a spike in wildlife poisoning events in 2015 (WCS, 2016), there was an acute need to understand poisoning cases and assess the impacts on Cambodian vulture populations. To this end, Loveridge *et al*. (2018) assessed the size and trends of Cambodian vulture populations and analysed the threats posed by poisoning. Their results indicated that after reaching a peak in 2013–2014, Cambodian vultures declined again due to secondary poisoning, from carbofuran specifically. This is one of the most toxic carbamate pesticides and was found in samples from six separate poisoning incidents, all of which were negative for organophosphates (WCS, 2016). They also estimated that the vulture population included at least 172 birds nationally in 2016 (-42% compared to 2010), comprising 109 white-rumped vultures (-46%), 37 slender-billed vultures (-23%) and 26 red-headed vultures (-45%) (Loveridge *et al*., 2018). In this paper, we provide updated information on the population size and trends of the three vulture species in Cambodia based on census data collected between 2014 and 2024. We also assess the effectiveness of ongoing conservation efforts.

Methods

Our study comprised data collected at four sites spanning the known range of vultures in Cambodia: the Siem Pang Wildlife Sanctuary (SPWS), Chhaeb-Preah Roka Wildlife Sanctuary (CPRWS), Srepok Wildlife Sanctuary (Eastern Plains Landscape, EPL) and the Mekong Flooded Forest (MFF). A vulture restaurant was established at each site to provide a consistent and uncontaminated source of food (comprising either cows or buffaloes) for the birds and monitor their population trends (Fig. 1).

The population data we present was obtained from simultaneous census counts undertaken from March 2014 to December 2024 and regular counts conducted from July 2016 to December 2024. Similar to Clements *et*

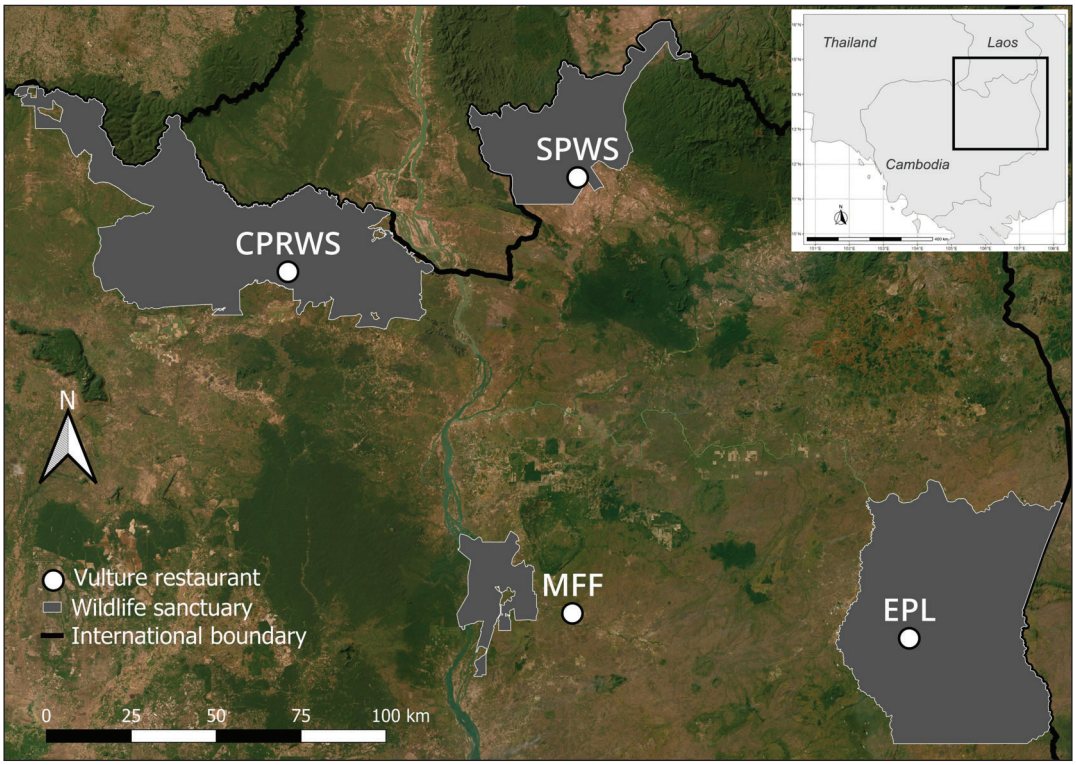

Fig. 1 Vulture restaurants in Cambodia: CPRWS=Chhaeb-Preah Roka Wildlife Sanctuary, SPWS=Siem Pang Wildlife Sanctuary, MFF=Mekong Flooded Forest (Sambor Wildlife Sanctuary), EPL=Eastern Plains Landscape (Srepok Wildlife Sanctuary)

al. (2013) and Loveridge *et al*. (2018), we only considered data on red-headed, slender-billed and white-rumped vultures (Fig. 2). Himalayan griffon vultures *Gyps himalayensis* and cinereous vultures *Aegypius monachus* were not considered because these are vagrant species in Cambodia (Goes, 2013).

Vulture population sizes & trends

To monitor vulture population size and trends, we used the same methodology as Clements *et al*. (2013) and Loveridge *et al*. (2018). Vulture populations were monitored through simultaneous censuses which were undertaken quarterly at the four sites and asynchronous counts made during regular feeding events at the vulture restaurants in the four study sites.

Simultaneous census counts

Five national censuses were undertaken annually. Each year, simultaneous censuses took place around 20 March, June, September and December, with an additional count around 10 June. The aim of the census was to coordinate simultaneous counts across protected areas in Cambodia and thereby monitor the size and distribution of their vulture populations. It also allows us to avoid duplicate counts and provide a minimum population estimate (MPE). For a given calendar year, we define the MPE as the highest total number of vultures observed across all sites during a single, simultaneous national census. This approach minimizes the risk of double-counts of birds moving between sites and is a conservative estimate of population size. It also allows us to calculate a specific MPE for each vulture species using only the highest population count for the individual species over the year.

Regular counts at vulture restaurants

Regular feeding events were conducted at three vulture restaurant sites (CPRWS, EPL & MFF) with at least one cow or buffalo carcass provided per month. At SPWS, feeding events were undertaken once a week in 2021 with cow carcasses (average weight 200 kg). These alternated between cow and buffalo carcasses every week in 2022 (average weight 297 kg), whereas only buffalo carcasses were provided each week from 2023 onwards (average weight 385 kg). At each feeding event, every vulture was recorded by species, age class (adult, subadult or juvenile) and sex (in the case of RHV). Feeding events undertaken between July 2016 and December 2024 are summarised in Table 1.

Data analysis

We fitted two sets of generalised linear models for each species: one based on data from the regular feeding counts and one based on data from the simultaneous census counts. We analysed data collected during restaurant feeding events between 10 July 2016 and 27 December 2024 and simultaneous census counts from March 2014 to December 2024 at all sites, excluding data from the fifth census undertaken around 10 June between 2016 and 2024. In 2014 and 2015, censuses were conducted around the 10th of the month each quarter with 20th June representing the fifth census, hence the latter was removed. Candidate models are listed in Table 2.

The parameters we used to evaluate the restaurant data were the same as those employed by Loveridge *et al*. (2018), whereas for census data, we modelled the total count across all sites as a function of either a linear or quadratic effect of date, with season as a fixed effect and interactions between them. Data were analysed using generalised linear models with quasi-Poisson errors and a log-link function in *R* vrs. 4.3.2 (R Core Team, 2023). The best models were chosen by selecting those with the lowest quasi-AICc (QAICc) scores, and we demonstrate the level of support for the top models by reporting QAICc weights and ΔQAICc scores (the difference between the specified model and the best model). To calculate QAICc scores and weights, we also re-ran all models with standard Poisson errors, and corrected

Table 1 Number of feeding events held at vulture restaurants at study sites each year from July 2016 to December 2024

Study sites	2016	2017	2018	2019	2020	2021	2022	2023	2024	Total
Siem Pang Wildlife Sanctuary	13	26	24	31	41	52	51	52	52	342
Chhaeb-Preah Roka Wildlife Sanctuary	11	41	36	50	37	24	36	40	43	318
Eastern Plains Landscape	6	13	13	13	11	11	11	8	8	94
Mekong Flooded Forest	2	11	12	13	12	12	9	12	12	95
Total	**32**	**91**	**85**	**107**	**101**	**99**	**107**	**112**	**115**	**849**

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Fig. 2 (top left) Vultures feeding on a carcass at a restaurant (© J.C. Eames); (top right) white-rumped vulture, slender-billed vulture and red-headed vulture (© R. Legrand); (bottom left) adult white-rumped vulture (© J.C. Eames); (bottom centre) adult female (black iris) and male (pale iris) red-headed vultures (© Wildlife Conservation Society, Cambodia); (bottom right) juvenile (front) and adult (rear) slender-billed vultures (© J.C. Eames)

Table 2 Candidate models fitted to count data from regular feeding events and simultaneous censuses at study sites

Data	Models
Regular feeding counts	date // date² // site // season // date x site // date² x site // site x season // date x season // date² x season // date x site x season // date² x site x season
Simultaneous census counts	date // date² // season // date x season // date² x season

AICc scores using the dispersion from the most complex model in each set (*date² x site x season*, and *date² x season*) using the *bblme* package in *R* (Bolker & R Development Core Team, 2024). Following Clements *et al*. (2013), we also performed an analysis of variance on the top model of the restaurant data to test the significance of the predictor variables.

Nest site monitoring

Similar to previous studies, vulture nesting sites at the four study sites were identified using local knowledge and systematic surveys from the end of the wet season in October till fledging in April. Depending on the site, the nests were monitored either by staff from partner organisation or local villagers who are rewarded for nest detection and successful fledging of young (Eang *et al*., 2021). Data on locations and vulture species are collected and reported by each organization before being collated.

Mortality events

Suspected poisoned animal carcasses were reported directly to local authorities following an agreed protocol. Poisoned carcasses and baits were destroyed by burning and poisoned waters were pumped out to prevent further vulture mortality. Where appropriate, dead vulture carcasses were sent to the Wildlife Conservation Society Wildlife Health programme for necropsy, although no toxicology testing has been undertaken since 2016.

Results

Vulture population sizes & trends

Simultaneous census counts

The highest census count in September 2024 indicated a minimum population of 14 red-headed vultures, 48 slender-billed vultures and 72 white-rumped vultures (Table 3). The top model for red-headed vultures was the *date x season* model, with a weight of 0.908 (Table 4). For slender-billed vultures, the two top models were the *season* and *date x season* models with weights of 0.416 and 0.380 respectively (Table 4). For white-rumped vultures, the top model was the *date²* model with a weight of 0.491 (Table 4). The model *date* also received a relatively high level of support for this species, with a weight and ΔQAICc of 0.336 and 0.76 respectively (Table 4). Expected counts for each species with 95% confidence intervals and the counts recorded in annual census counts are shown in Fig. 3. Coefficient estimates in Table 5 show the magnitude and significance of each predictor variable in these models, with the effect of season relative to dry as the reference season.

Red-headed vulture counts show a marked downward trend over the last ten years. The minimum population estimate decreased from 23 birds in 2014 to 14 birds in the first half of 2024 (equivalent to -4% annually over ten years). Counts for slender-billed vultures appeared to be stable between 2014 and 2024. Counts of white-rumped vultures declined from 2014 onwards and then rose in recent years. A steady decline was observed from 139 birds in 2014 to 66 birds in 2018, followed by an increase which reached 78 birds in June 2024.

Regular counts at vulture restaurants

Numbers of all three vulture species appeared to fluctuate over time and between sites (Table 6). Overall, populations of the three species are either stable or declining slightly.

Counts for all three species were best modelled by *date² × site × season*. This model was the best supported for all three species and had the highest QAICc weight among the candidate models (with weight of 0.992 for red-headed vultures and 1.0 for slender-billed and white-rumped vultures: Table 7). Analysis of variance in count data showed that the effects of the quadratic function of time, the effect of site, and the interaction between site and season were highly significant for all species, whereas the effect of season was only significant for red-headed vultures. The interaction term for date with site was significant for red-headed and slender-billed vultures, whereas the interaction term for date with season was only significant for white-rumped vultures. Finally, the three-way interaction was significant for slender-billed and white-rumped vultures (Table 6). Expected counts for each species with 95% confidence intervals and the actual restaurant counts recorded at each site are shown in Fig. 4. Coefficient estimates in Table 8 indicate the magnitude and significance of each predictor variable in

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Table 3 Results of simultaneous census counts undertaken from March 2014 to December 2024 across all study sites

Year	Minimum Population Size			
	RHV	SBV	WRV	Total
March 2014	22	27	91	**140**
June 2014 (1st event)	23	52	139	**214**
June 2014 (2nd event)	16	50	127	**193**
September 2014	18	41	54	**113**
December 2014	10	23	94	**127**
March 2015	15	36	82	**133**
June 2015 (1st event)	15	47	91	**153**
June 2015 (2nd event)	18	34	73	**125**
September 2015	20	25	76	**121**
December 2015	16	28	83	**127**
March 2016	14	22	8	**44**
June 2016 (1st event)	26	18	72	**116**
June 2016 (2nd event)	26	37	109	**172**
September 2016	23	32	82	**137**
December 2016	19	32	81	**132**
March 2017	20	31	84	**135**
June 2017 (1st event)	12	15	43	**70**
June 2017 (2nd event)	10	33	78	**121**
September 2017	19	36	27	**82**
December 2017	22	29	59	**110**
March 2018	12	27	46	**85**
June 2018 (1st event)	17	35	66	**118**
June 2018 (2nd event)	21	31	69	**121**
September 2018	22	32	87	**141**
December 2018	12	25	54	**91**
March 2019	8	32	73	**113**
June 2019 (1st event)	14	25	57	**96**
June 2019 (2nd event)	21	28	70	**119**
September 2019	16	43	78	**137**
December 2019	13	35	54	**102**
March 2020	6	28	36	**70**
June 2020 (1st event)	11	37	71	**119**
June 2020 (2nd event)	15	43	71	**129**
September 2020	16	36	70	**122**
December 2020	14	28	71	**113**
March 2021	10	28	60	**98**
June 2021 (1st event)	13	27	42	**82**
June 2021 (2nd event)	20	35	66	**121**
September 2021	14	15	46	**75**
December 2021	18	22	49	**89**
March 2022	11	33	55	**99**
June 2022 (1st event)	19	42	73	**134**
June 2022 (2nd event)	21	32	75	**128**
September 2022	15	30	61	**106**
December 2022	11	32	66	**109**
March 2023	8	30	76	**114**
June 2023 (1st event)	12	42	76	**130**
June 2023 (2nd event)	14	37	81	**132**
September 2023	13	12	37	**62**
December 2023	13	43	75	**131**
March 2024	7	47	76	**130**
June 2024 (1st event)	13	38	78	**129**
June 2024 (2nd event)	14	27	60	**101**
September 2024	14	48	72	**134**
December 2024	11	19	43	**73**

these models, with the effect of sites relative to CPRWS as the reference site and dry as the reference season.

The highest number of slender-billed and white-rumped vultures were recorded at SPWS (Fig. 4), as shown by the positive coefficient estimates for the site effect of SPWS relative to CPRWS (Table 8). SPWS and CPRWS are clearly the most important sites for these two species, because very few individuals have been recorded in EPL and MFF over the past decade. Numbers of white-rumped vultures in CPRWS and SPWS appeared to decline between 2016 and 2020 and increase from 2020 onwards (Fig. 4), as indicated by the significance of the *date* and *date*^{2} models. Slender-billed vultures seemed to follow the same trajectory in SPWS, though the *date* and *date*^{2} models were not significant for the species. Numbers of slender-billed vultures recorded in CPRWS also seemed to trend upwards in the 2016-2024 period (Fig. 4). Our results suggest that higher numbers of white-rumped and slender-billed vultures are counted during the dry season (Table 8).

Numbers of red-headed vultures appear to be more evenly distributed across the restaurants at our study

Table 4 Model sets, ΔQAICc scores and model weights for simultaneous census counts at all study sites

Model	ΔQAICc	Degrees of freedom	Weight
Red-headed vultures			
Date x season	0	4	0.908
Date^2 x season	5.02	6	0.074
Season	9.20	2	0.009
Date	9.85	2	0.007
Date^2	12.06	3	0.002
Slender-billed vultures			
Season	0	2	0.416
Date x season	0.19	4	0.380
Date	2.84	2	0.101
Date^2	4.11	3	0.053
Date^2 x season	4.24	6	0.050
White-rumped vultures			
Date^2	0	3	0.491
Date	0.76	2	0.336
Date x season	3.23	6	0.098
Season	4.98	2	0.041
Date^2 x season	5.32	6	0.034

sites, with none supporting more than 15 birds. CPRWS appears to show a pattern of decline, whereas populations in SPWS and MFF appear to be more constant. In 2016, EPL had lower numbers of red-headed vultures than CPRWS, as indicated in the negative coefficient estimate for the site effect of EPL. However, counts for the site suggest an upward trend in recent years. Numbers of red-headed vultures recorded in the wet season were estimated to be significantly higher (Table 8).

Nest monitoring

Nests of all three species were mainly found in or near SPWS, which accounted for more than 80% of all nests found during the 2022–2023 season. Fledgling success at all sites initially decreased during the study period, before increasing from 2021 onwards. In every case, only one chick was observed per nest (Table 9). In SPWS, 2–3 nests of red-headed vultures and 6–11 nests of slender-billed vultures were found annually in the last five years of the study period.

Between two and four nests of red-headed vultures were found each year in CPRWS, all of which were in dipterocarp trees. A slender-billed vulture nest was found for the first time in CPRWS in 2022–2023, although white-rumped vulture nests have not been found at the site since 2016–2017.

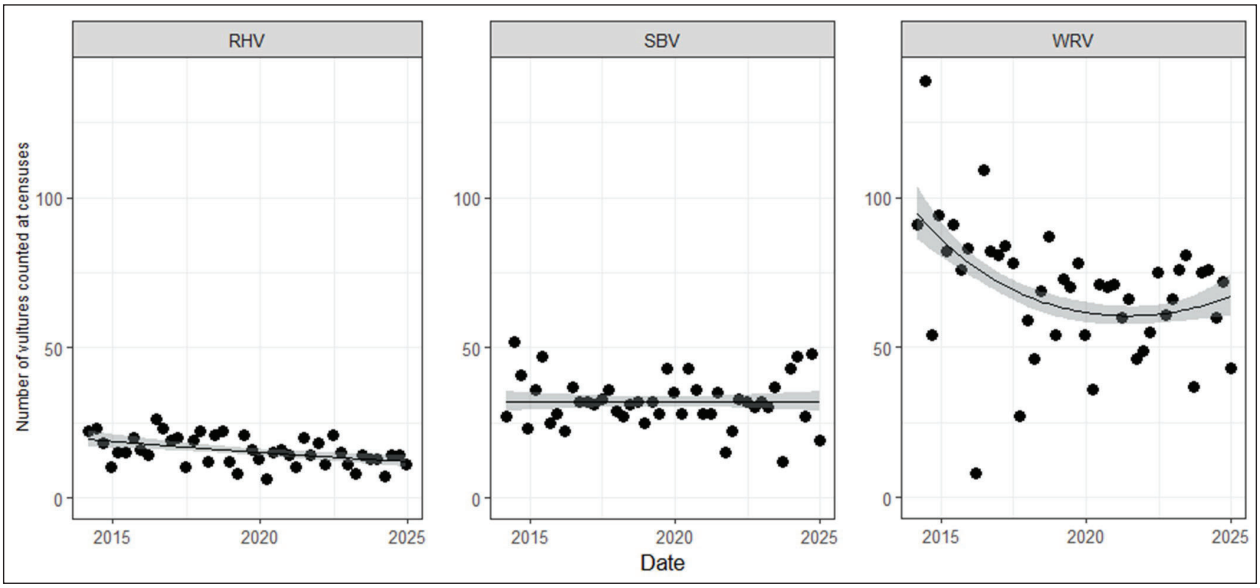

Fig. 3 Counts of red-headed vultures (RHV), slender-billed vultures (SBV) and white-rumped vultures (WRV) at annual census counts at restaurant sites between March 2014 and December 2024 (points), with estimated count from top models (lines) and 95% confidence intervals (grey shading)

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Table 5 Coefficient estimates from generalized linear models of vultures at census counts at all sites, with dry used as the reference season. [A] denotes $p<0.05$, [B] $p<0.001$ and [C] $p<0.001$

Parameter	Estimate	St. Error	*t*	*p*
Red-headed vultures				
Intercept	2.88	1.50^{E-01}	19.26	$<2^{E-16}$ [C]
Date	-1.73^{E-04}	1.87^{E-04}	-0.92	0.36
Date²	5.22^{E-09}	4.79^{E-08}	0.11	0.91
SeasonWet	1.06^{E-01}	2.05^{E-01}	0.52	0.61
Date x seasonWet	1.92^{E-04}	2.54^{E-04}	0.75	0.45
Date² x seasonWet	-3.56^{E-08}	6.45^{E-08}	-0.55	0.58
Slender-billed vultures				
Intercept	3.32	1.60^{E-01}	20.78	$<2^{E-16}$ [C]
Date	9.91^{E-06}	1.83^{E-04}	0.05	0.96
Date²	1.02^{E-08}	4.44^{E-08}	0.23	0.82
SeasonWet	4.90^{E-01}	2.10^{E-01}	2.33	0.25 [A]
Date x seasonWet	-2.90^{E-04}	2.49^{E-04}	-1.16	0.25
Date² x seasonWet	4.06^{E-08}	6.14^{E-08}	0.66	0.51
White-rumped vultures				
Intercept	4.48	1.63^{E-01}	27.51	$<2^{E-16}$ [C]
Date	-3.77^{E-04}	2.01^{E-04}	-1.88	0.07
Date²	8.09^{E-08}	4.99^{E-08}	1.62	0.11
SeasonWet	1.42^{E-01}	2.25^{E-01}	0.63	0.53
Date x seasonWet	8.02^{E-05}	2.80^{E-04}	0.29	0.78
Date² x seasonWet	-3.44^{E-08}	7.03^{E-08}	-0.49	0.63

Table 6 Analysis of variance for generalized linear models of red-headed vulture (RHV), slender-billed vulture (SBV) and white-rumped vulture (WRV) numbers at restaurants. [A] denotes $p<0.05$, [B] $p<0.001$ and [C] $p<0.001$

Variable	Degrees of freedom	F (significance)		
		RHV	SBV	WRV
Date²	2	6.81 [B]	75.88 [C]	77.45 [C]
Site	3	67.60 [C]	945.44 [C]	1075.69 [C]
Season	1	75.26 [C]	1.01	2.57
Date² x site	6	20.90 [C]	8.31 [C]	0.90
Date² x season	2	2.02	2.35	3.72 [A]
Site x season	3	6.71 [C]	11.24 [C]	13.81 [C]
Date² x site x season	6	1.61	4.13 [C]	3.73 [B]

Table 7 Model sets, ΔQAICc scores and model weights for regular feeding counts at all study sites

Model	ΔQAICc	Degrees of freedom	Weight
Red-headed vultures			
Date² x site x season	0	24	0.992
Date x site x season	9.74	16	0.0086
Date² x site	80.76	12	0
Date x site	90.36	8	0
Site x season	123.20	8	0
Site	214.43	4	0
Date x season	339.14	4	0
Date² x season	342.06	6	0
Season	348.34	2	0
Date	392.86	2	0
Date²	393.76	3	0
Slender-billed vultures			
Date² x site x season	0	24	1
Date x site x season	32.73	16	0
Date² x site	39.05	12	0
Date x site	62.03	8	0
Site x season	69.98	8	0
Site	99.49	4	0
Date x season	2891.89	4	0
Date² x season	2894.17	6	0
Date	2905.15	2	0
Date²	2906.93	3	0
Season	3043.61	2	0
White-rumped vultures			
Date² x site x season	0	24	1
Date x site x season	30.80	16	0
Date² x site	48.77	12	0
Site x season	52.39	8	0
Date x site	77.64	8	0
Site	88.23	4	0
Date² x season	3255.24	6	0
Date²	3262.76	3	0
Date x season	3273.69	4	0
Date	3283.04	2	0
Season	3402.81	2	0

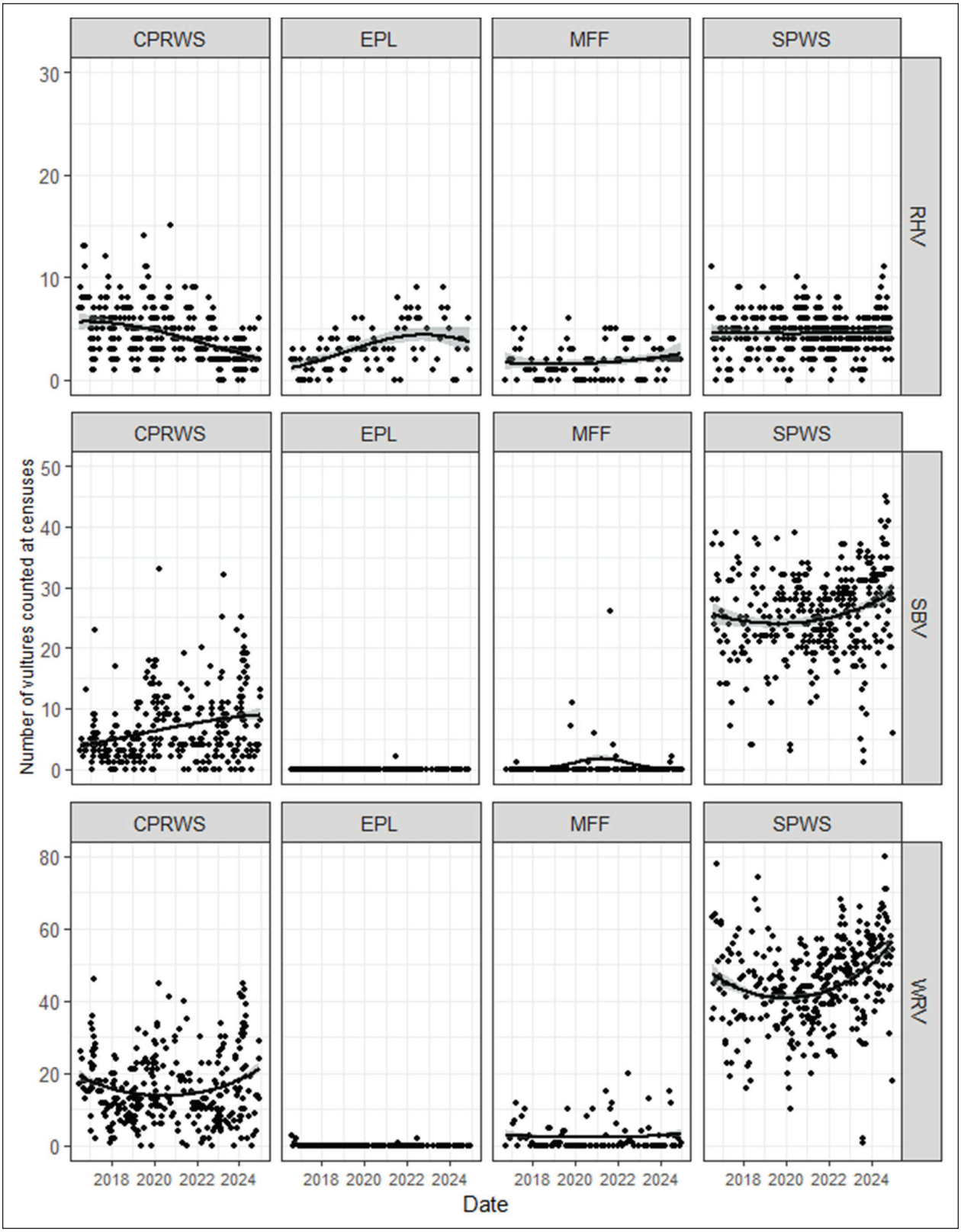

Fig. 4 Counts of red-headed (RHV), slender-billed (SBV) and white-rumped vultures (WRV) at four vulture restaurants from July 2016 to December 2024 (points), with 95% confidence interval for top models (lines). Due to rarity of SBV and WRV records at study site in the Eastern Plains Landscape, only the actual restaurant counts are indicated

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Table 8 Coefficient estimates from generalized linear models of numbers of vultures recorded at restaurants, with CPRWS as reference site and dry as the reference season. [A] denotes $p<0.05$, [B] $p<0.001$ and [C] $p<0.001$

Parameter	Estimate	Standard Error	*t*	*p*
		Red-headed vultures		
Intercept	1.49	1.13^{E-01}	13.22	$<2^{E-16}$ [C]
Site-EPL	-1.72	3.92^{E-01}	-4.40	1.22^{E-05} [C]
SeasonWet	5.37^{E-07}	1.54^{E-01}	3.48	0.00053 [C]
Date x site-EPL	-1.51^{E-03}	5.20^{E-04}	2.90	0.0039 [B]
Date x site-MFF	-1.31^{E-03}	6.44^{E-04}	-2.04	0.042 [A]
Date² x site-M qFF	4.96^{E-07}	1.97^{E-07}	2.52	0.012 [A]
Date² x site-SPWS	1.72^{E-07}	7.85^{E-08}	2.19	0.028 [A]
Site-MFF xseasonWet	-1.23	5.95^{E-01}	-2.07	0.038 [A]
Site-SPWS x seasonWet	-6.37^{E-01}	2.39^{E-01}	-2.67	0.0078 [B]
		Slender-billed vultures		
Intercept	1.57	1.68^{E-01}	9.30	$<2^{E-16}$ [C]
Site-SPWS	1.52	1.98^{E-01}	7.66	5.04^{E-14} [C]
SeasonWet	-8.74^{E-01}	3.24^{E-01}	-2.69	0.0072 [B]
Date x seasonWet	1.52^{E-03}	4.56^{E-04}	3.34	0.00086 [C]
Date² x seasonWet	-5.86^{E-07}	1.41^{E-07}	-4.15	3.73^{E-05} [C]
Site-SPWS x seasonWet	1.15	3.51^{E-01}	3.28	0.0011 [B]
Date x site-SPWS x seasonWet	1.71^{E-03}	4.89^{E-04}	-3.51	0.00048 [C]
Date² x site-SPWS x seasonWet	6.28^{E-07}	1.51^{E-07}	4.17	3.32^{E-05} [C]
		White-rumped vultures		
Intercept	3.11	1.07^{E-01}	29.02	$< 2^{E-16}$ [C]
Date	-7.09^{E-04}	1.65^{E-04}	-4.30	1.89^{E-05} [C]
Date²	2.54^{E-07}	4.99^{E-08}	5.09	4.47^{E-07} [C]
Site-MFF	-1.44	6.33^{E-01}	-2.28	0.023 [A]
Site-SPWS	6.79^{E-01}	1.38^{E-01}	4.89	1.21^{E-06} [C]
SeasonWet	-4.36^{E-01}	1.83^{E-01}	-2.38	0.017 [A]
Date x site-SPWS	4.44^{E-04}	2.01^{E-04}	2.21	0.027 [A]
Date² x site-SPWS	-1.45^{E-07}	6.03^{E-08}	-2.40	0.016 [A]
Date x seasonWet	8.53^{E-04}	2.87^{E-04}	2.97	0.0031 [A]
Date² x seasonWet	-3.54^{E-07}	9.25^{E-08}	-3.83	0.00014 [C]
Site-SPWS x seasonWet	5.73^{E-01}	2.17^{E-01}	2.65	0.0083 [B]
Date x site-SPWS x seasonWet	-8.04^{E-04}	3.25^{E-04}	-2.47	0.014 [A]
Date² x site-SPWS x seasonWet	3.27^{E-07}	1.03^{E-07}	3.18	0.0015 [B]

Table 9 Vulture nests and the number of chicks known to have fledged across all study sites between 2011 and 2023

Year	Red-headed vultures		Slender-billed vultures		White-rumped vultures		Overall fledging success (%)
	Nests	Fledged	Nests	Fledged	Nests	Fledged	
2011–12	3	1	3	3	7	7	85
2012–13	1	1	11	8	13	12	84
2013–14	1	1	12	10	6	5	84
2014–15	3	3	18	11	6	5	70
2015–16	6	6	6	4	3	1	73
2016–17	10	8	10	7	2	1	73
2017–18	10	7	10	7	1	1	71
2018–19	8	5	10	8	1	0	68
2019–20	6	3	6	5	2*	2	71
2020–21	7	4	7	5	0	0	64
2021–22	5	4	9	8	4*	4	89
2022–23	6	5	12	8	12*	9	85
2023–24	6	6	13	11	≥16**	16	89
Total	**72**	**54**	**127**	**95**	**73**	**63**	

* Nests counted at the breeding colony in Lao PDR, 25 km away from the vulture restaurant in SPWS

** Number inferred from the maximum number of young recorded at the same time at SPWS vulture restaurant in 2024, as no survey of the breeding colony was conducted that year

Table 10 Number of suspected or confirmed poisoned carcasses and poisoning events reported to the Cambodian Vulture Working Group between 2016 and 2024 (several carcasses can be linked to a single poisoning event)

Study sites	2016	2017	2018	2019	2020	2021	2022	2023	2024	Total
Number of ungulate carcasses	NA	NA	NA	NA	5	0	5	6	12	**28**
Number of events	4	2	2	3	11	0	2	8	2	**34**

Table 11 Recorded incidences of vulture mortality in Cambodia from 2016 to 2024

Date	Cause of mortality	Red-headed vultures	Slender-billed vultures	White rumped vultures
February 2019	Unknown		1	
July 2019	Hunted			1
June 2020	Unknown	1		
May 2020	Euthanized	1		
February 2021	Debilitation			
April 2022	Unknown			1
August 2022	Unknown			1
November 2022	Head Trauma	1		
March 2024	Unknown	1		
December 2024	Unknown			1
	Total	**4**	**1**	**4**

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Mortality events

A total of 34 poisoning events were reported to the Cambodia Vulture Working Group (CVWG) between 2016 and 2024, with at least 28 associated with ungulate carcasses (Table 10). These spiked in 2020 when 11 poisoning cases occurred in and around CPRWS, eight of which contained carbofuran and the remaining three unknown poisons. The offenders mixed the poison with rice and other food (e.g., frogs) and placed it as bait at water bodies such as streams and seasonal wetlands. In these poisoning events, vultures are not specifically targeted but could have fallen victim to secondary poisoning because some cows died. No vulture deaths were reported from these events, although other wildlife deaths did occur (Broadis & Ny, 2021). Ten vulture deaths were reported over the same period, including four red-headed vultures, four white-rumped vultures, one slender-billed vulture (Table 11), and one Himalayan griffon vulture. However, none of these could be confidently linked to poisoning, either intentional or secondary.

Discussion

Vulture population sizes & trends

Loveridge *et al*. (2018) concluded that populations of all three vultures were declining in Cambodia due to secondary carbofuran poisoning. This carbamate pesticide was found in samples taken from six separate wildlife poisoning incidents in 2016, whereas organophosphates were not detected (WCS, 2016). While this conclusion remains tentative due to the small sample size and additional testing is needed to better understand the scale and nature of this threat, these findings nonetheless guided conservation management efforts subsequently undertaken for vulture species in Cambodia. These included supplementary feeding through weekly or monthly vulture restaurants, both as a means of mitigating low natural food availability (García-Ripollés *et al*., 2004) and reducing exposure to poisoned carcasses (Gilbert *et al*., 2007). From 2016 to 2024, an average of 94 carcasses were provided per year at the vulture restaurants, mostly in SPWS and CPRWS (over 75% of the total for both sites combined).

Coordinated censuses during these events provided a way of monitoring vulture populations, as a minimum population estimate could be derived from the highest total from all sites combined for a given year, and a specific MPE could be calculated for each species taking only the highest population count for that species over the year. In 2024, the MPE was 134 vultures (comprising 78 white-rumped vultures, 48 slender-billed vultures & 14 red-headed vultures). This is stable compared to the MPE of 132 vultures in 2023 (81 white-rumped vultures, 43 slender-billed 132 & 14 red-headed vultures) and 134 in 2022 (75 white-rumped vultures, 42 slender-billed vultures & 21 red-headed vultures) (Gray-Read & Ny, 2023, 2024). According to current estimates, the Cambodian population accounts for a maximum of 1.30% of the global population of white-rumped vultures, 4.36% of slender-billed vultures and 0.40% of red-headed vultures (BirdLife International, 2024).

Following the marked decline suggested by Loveridge *et al*. (2018), our study suggests that the decline of the three vulture species has slowed down, although the threat of secondary poisoning remains of critical importance. Data from SPWS and CPRWS indicate that white-rumped vultures declined steadily until 2019 then increased from 2020 onwards. This corresponds to the increased frequency of feeding at vulture restaurants in SPWS and greater quantity of food provided (from weekly one cow carcass averaging 200 kg to one buffalo carcass averaging 400 kg). Similarly, census numbers of slender-billed vultures appeared stable between 2014 and 2024, whereas red-headed vultures appeared to slightly decrease each year according to census figures. This decline was largely driven by a decrease in CPRWS, which was not compensated by the increases seen in EPL and MFF. The population of red-headed vultures appears to be stable in SPWS.

The reasons for the continuous decline of red-headed vultures compared to increases or stabilisation of populations of white-rumped and slender-billed vultures in recent years are not known but could be related to their behaviour. Unlike the latter which are gregarious, red-headed vultures are most often solitary or found in breeding pairs. Their patchy distribution and territorial behaviour could explain the slight decline observed, because only four sites maintained monthly vulture restaurants in our study period, as opposed to five in Loveridge *et al*. (2018) and seven in Clements *et al*. (2013). Sites in the eastern plains landscape (namely Lomphat Wildlife Sanctuary, Srepok Wildlife Sanctuary and Sesan River area) already had lower numbers of all species by 2016, having experienced a steeper decline compared to northern sites (Loveridge *et al*., 2018). The decrease in numbers of *Gyps* spp. attending vulture restaurants eventually led to their closure at these sites. Data collected before this suggest that the sites supported red-headed vultures more regularly and that the cessation of feeding contributed to local declines (CVWG, unpubl. data).

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In assessing population trends, it should be noted that red-headed vultures may not rely on supplementary feeding to the same extent as the other two species. The feeding behaviour of the three species may also differ at vulture restaurants (Moreno-Opo *et al*., 2015; Loveridge *et al*., 2018). Overall, the range of the three vulture species continued to contract, with the two most northerly sites, SPWS and CPRWS, recording the highest numbers of vultures each year. These two sites collectively account for 89% of all vultures censused in 2021 and 2022, 92% in 2023 (with SPWS accounting for 69% and CPRWS for 23%) and 91% in 2024 (SPWS accounting for only 62% [due to unusually low numbers in the December census] and CPRWS for 28%) (Broadis *et al*., 2022; Gray-Read & Ny, 2023, 2024). Whether the observed range contraction is a consequence of the increased food availability at these two sites is unknown. Since the two sites are only 90 km apart, their proximity implies that they could influence each other, as tagged vultures are frequently recorded flying from one site to another in the space of a few hours (Rising Phoenix, unpubl. data).

Finally, based on discussions of energetic requirements in Clements *et al.* (2013), the 49 buffalo (mean weight 385 kg) and six cow carcasses (mean weight 200 kg) provided in SPWS in 2024, coupled with the five buffalo and 38 cow carcasses provided that year in CPRWS, represented 29,500 kg of carcasses in total (and 28,000 kg in 2023). According to Swan *et al*. (2006), a white-rumped vulture requires 0.341 kg of ungulate tissue per day. If 77% of carcasses are available to vultures (Green *et al*., 2006), then the food provided at these two sites would have been sufficient to support 183 vultures in 2024 (and 173 vultures in 2023). Although theoretical, these calculations suggest that current levels of feeding provided at the vulture restaurants could effectively address the reduced food availability associated with the decline of ungulate populations in Cambodia. This could help to explain the various trends observed in vulture populations observed in our study.

Nest monitoring

SPWS is a major site for vulture breeding in Cambodia, being the only site where nests of all three species are detected yearly and it accounts for most of the nests monitored nationally. To encourage vultures feeding at the restaurant in SPWS to nest within the sanctuary, 21 artificial nesting platforms were created in 2020 and 2021, at heights of 15-20 m from the ground in dipterocarp trees up to 25 m high. These were located 150 to 1,000 metres from the restaurants. Since then, one of the platforms has been occupied by a pair of slender-billed vultures and successfully fledged one young for three consecutive years (Rising Phoenix, unpubl. data). Two white-rumped vultures fitted with GPS-GSM trackers (OrniTrack-50, Ornitela, Lithuania) in 2020 confirmed the existence of a breeding colony in Lao PDR just 25 km from the vulture restaurant where 12 active WRV nests were counted in 2023 (Legrand *et al*., 2024). It is unknown whether the establishment of this colony predates the provision of carcasses at SPWS. Aside from this colony, the last nests recorded of white-rumped vultures in Cambodia were found in the MFF during the 2018–2019 breeding season. Tracking data from birds tagged with GPS-GSM trackers indicate that the white-rumped vultures spend most of their time ranging in northern Cambodia (Rising Phoenix, unpubl. data), often roosting at the colony in Lao PDR. Given the rarity of records of the species at restaurants other than SPWS and CPRWS, it is reasonable to assume that most nests are concentrated there.

Illegal forest clearance in vicinity of nesting sites may be the main threat to vultures in CPRWS, because it causes disturbance and can lead to nest abandonment. Monitoring data from the Northern Plains Landscape from 2008 to 2016 have shown that logging of tall nesting trees—driven largely by land concessions—posed a serious threat to large bird species, including vultures (Harrison & Mao, 2017). Data collected more recently by monitoring teams in CPRWS includes evidence of illegal logging near active nesting sites, indicating continued pressure on nesting habitats (WCS, unpubl. data).

The 13 nests of slender-billed vultures monitored in 2023–24 is the highest documented since the 2014–15 breeding season, when 18 nests were recorded. This result of 26 breeding adults is consistent with the MPE of 43 birds reported in 2023 (Gray-Read & Ny, 2024). Given that up to 32 adults were recorded at the same feeding event in SPWS in 2024 (Rising Phoenix, unpubl. data), it is likely that the majority of slender-billed vulture nests were monitored that year, with only a few escaping detection. The observed nesting success of more than 65% for the two *Gyps* species is greater than the 50% reported for white-rumped vultures in India and Nepal by Baral *et al*. (2005) and Thakur (2015) and similar to the 73% reported by Thakur & Narang (2012).

One to two nests of red-headed vultures are usually reported each year at EPL & MFF (Broadis & Ny, 2021, 2020; Broadis *et al*., 2022; Gray-Read & Ny, 2019, 2023, 2024). Due to their territorial behaviour, we expect nests of red-headed vultures would be more dispersed in the landscape. The number of nests recorded for the species was again consistent with the number of birds counted at each site, although it is also possible that the population size was under-represented in censuses and that additional nests exist in less surveyed areas.

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Mortality events

The poisoning of waterholes with pesticides and specifically carbofuran and other toxic substances remains an ongoing issue for vulture conservation in Cambodia. Local people often poison water sources to indiscriminately kill wildlife to collect and sell the meat. Vultures then become victims of secondary poisoning when they consume carrion. In 2015, one poisoned slender-billed vulture individual tested positive for carbofuran in toxicology tests. This was the first evidence of a vulture mortality due to carbofuran in Cambodia (Loveridge *et al*., 2018). Carbofuran is a highly toxic compound with a median lethal dose (LD50, the dose at which a substance is lethal for 50% of animals tested) value when ingested between 1 and 20 mg/kg in several mammal species (Gupta, 1994). The high toxicity of carbofuran and its widespread use to poison wildlife has prompted calls for its inclusion on lists of pesticides banned in Cambodia and Lao PDR.

Conservation perspectives

Vulture populations in Cambodia decreased until 2019 and have since shown signs of stabilization or slight recovery. Average productivity (fledglings per monitored pair) since the 2019–20 breeding season has been 0.79 for slender-billed vultures and 0.74 for red-headed vultures. Data for white-rumped vultures are incomplete due to the location of the breeding colony outside Cambodia and limited monitoring in recent years. All three species typically raise one chick per nest, a trait which is consistent across their global ranges (del Hoyo *et al*., 1994; Pain *et al*., 2003).

The three vulture species are long-lived (with lifespans of up to 20 years) and experience delayed maturity (with first reproduction at 5–7 years) and long generation lengths: 11.5 years for red-headed vultures, 12.0 years for slender-billed vultures and 11.3 years for white-rumped vultures (del Hoyo *et al*., 1994; Bird *et al*., 2020). Mortality is greatest in juvenile birds and reduces as these become sub-adults, with under 5% mortality annually estimated for adults in the wild (Prakash *et al*., 2012).

Productivity likely varies between species, with values between 0.5 and 0.73 reported for white-rumped vultures in India and Nepal (Baral *et al*., 2005; Thakur & Narang, 2012; Thakur, 2015; Bhusal *et al*., 2023;). Between 2011 and 2024 in Cambodia, average productivity was 0.75 fledglings per pair for slender-billed and red-headed vultures. Productivity for white-rumped vultures averaged 0.77 between 2011 and 2018, after which nest monitoring was limited by the relocation of breeding colonies outside Cambodia.

While modelling of population growth is beyond the scope of this paper, demographic parameters could help to illustrate why vulture populations recover slowly, even under favourable conditions. Assuming a life expectancy of 20 years, an age of first reproduction of six years, an annual mortality rate of 5% for adults and 20% for subadults (Mallord *et al*., 2024), a productivity rate of 0.75 and a fledging rate of 1, a stage-classified projection model or a Leslie matrix (Caswell, 2006) would give an estimated population growth rate of approximately 3–6% annually. This varies depending on the assumed proportion of potential breeders that skip reproduction annually. Population growth in long-lived species is generally highly sensitive to changes in adult survival rates (Schaub *et al*., 2009), and even modest increases in adult mortality could result in population decline. It is therefore not unexpected that the recovery of Cambodia's vulture populations remains slow, even under favourable conditions. Sustained conservation efforts will be essential in the long-term to maintain and support any recovery. Additionally, expansion of the current tagging programme is crucial to improve demographic data for vultures—particularly on survival rates—and refine population models for future conservation planning.

It remains uncertain whether Cambodia's red-headed vulture population is self-sustaining due to its small size and absence of long-term demographic data. A population viability analysis would be valuable to assess extinction risk and guide future management. Although no ex-situ or reinforcement programmes currently exist, these may become necessary if natural recruitment continues to decline. However, the development of these initiatives would require significant external support beyond the current efforts at SPWS and CPRWS.

Conclusions

Supplementary feeding at vulture restaurants has been effective in mitigating the impacts of secondary poisoning and natural food scarcity and halted the decline of slender-billed and white-rumped vultures in Cambodia. The only sites where supplementary feeding is regularly provided, SPWS and CPRWS, are now the major sites for vulture conservation nationally. SPWS hosts most of the known population and is the only site where nests of all three species are found. This is attributable to the weekly feeding programme undertaken at the site. However, the range contractions and subsequent concentration of vulture populations around these sites increases their vulnerability to catastrophic poisoning events. Conversely, vultures ranging more widely in the

landscape are vulnerable to a variety of additional causes of mortality, including collisions with power lines.

Cambodian vultures are now conservation dependent. The high proportion of vultures regularly recorded at CPRWS and SPWS indicates that most vultures in the country regularly feed on provisioned food. In the absence of this, vultures would almost certainly decline in Cambodia and most probably to national extinction because large wild ungulates have also decreased and increasing numbers of commercially-raised cattle are stall fed.

Providing fresh cow and buffalo carcasses is costly. The weekly provision of buffalo carcasses at SPWS costs approximately $40,000 USD per year and costs for supplementary feeding of Cambodian vultures are currently borne by just three organizations: Rising Phoenix, Wildlife Conservation Society and World Wide Fund for Nature. Withdrawal of any of these organizations would almost certainly have major implications for vulture survival in country.

Regular provision of carcases at vulture restaurants in key sites is essential to the survival of vulture populations in Cambodia. Innovative ways to improve nesting success should be explored. A ban on carbofuran ban should be sought to address the threat posed by poisoning, along with ways to ensure that this is effectively implemented. Continued monitoring is also essential.

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