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Continued population recovery and high annual survival rates of White-rumped Vultures in Nepal

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Populations of *Gyps* vultures in South Asia underwent catastrophic declines caused by unintentional poisoning by the veterinary drug diclofenac. Since the drug was banned in 2006–2010, declines have halted across the region, including in Nepal. The present study updates population trends of *G. bengalensis* in Nepal based on recent road transect surveys. The population has continued to increase at a rate of 12.7% per annum since the population low point in 2012. Assuming an age of first breeding (α) of 4 years, we composed a simple age-structured Leslie population matrix model, which was parameterized using estimates of annual survival of adult and immature GPS-tagged birds (0.947 and 0.955, respectively), and juveniles (0.65) of the related *G. fulvus*, and productivity figures from annual nest monitoring across Nepal (0.69 fledglings per nest per year). The intrinsic rate of population increase during the population recovery (λ (95% confidence limits)) estimated from the matrix model was 1.087 (1.033, 1.127) (i.e. 8.7% increase per annum). Values of λ were 1.099 and 1.075 for $\alpha = 3$ and 5 years, respectively. The estimate of λ derived from the Demographic Invariants Method, utilizing estimates of annual adult survival and α (4 years), was 1.097, that is 9.7% increase per annum ($\lambda = 1.116$ and 1.084 for $\alpha = 3$ and 5 years, respectively). The matrix-derived estimate of λ was more sensitive to changes in adult survival than any other demographic rate. Given the non-significant differences in the estimates of λ, there is no conclusive evidence that the recovery has been augmented by immigration from India. There was no evidence that variation in population trends across Nepal was associated with proximity to supplementary food. Numbers of vultures are still low relative to predecline levels, so actions to improve regulations and restrict the availability of vulture-toxic NSAIDs remain high conservation priorities.

Keywords: diclofenac, GPS/PTT tracking, *Gyps bengalensis*, intrinsic rate of population increase, Leslie matrix models, scavengers.

Starting in the mid-1990s, White-rumped *Gyps bengalensis*, Indian *Gyps indicus* and Slender-billed Vultures *Gyps tenuirostris*, endemic to South and South-east Asia, underwent catastrophic population declines. In India, all three species declined by more than 97%, with White-rumped Vulture declining by 99.9% between 1992 and 2007 (Prakash *et al.* 2007). In Nepal, this species declined by 91% over the same period (Chaudhary *et al.* 2012). Their global conservation status in the IUCN Red List was therefore changed from Least Concern to Critically Endangered (Birdlife International, 2021). The cause of these declines was unintentional poisoning by veterinary use of the non-steroidal anti-inflammatory drug (NSAID) diclofenac. When vultures fed from carcasses of cattle dosed with the

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drug soon before the animal died, they suffered kidney failure, visceral gout and death within a few days (Oaks *et al.* 2004, Shultz *et al.* 2004, Green *et al.* 2006, Swan *et al.* 2006). In response to publication of evidence indicating the role of diclofenac in the vulture declines, the governments of India, Pakistan and Nepal banned its veterinary use in 2006, followed by Bangladesh in 2010 (Prakash *et al.* 2007, Sarowar Alam 2017).

Following the ban on diclofenac, Vulture Safe Zones (VSZs) were established, in which conservation actions could be concentrated (Bowden *et al.* 2025). Such actions include advocacy and education aimed at all major stakeholders, including government officials, drug controllers, pharmacists, veterinarians and livestock owners. These efforts are intended to raise awareness of the ban on diclofenac, explain the threat posed by the drug and other NSAIDs to vultures, and promote the use of meloxicam (and more recently tolfenamic acid), which are the only NSAIDs so far shown to be safe for vultures (Bhusal 2018). Subsequent monitoring has demonstrated that there has been a reduction in the availability of diclofenac throughout the region, but especially in Nepal, where sales of the drug for veterinary use had all but ceased by about 2013 (Galligan *et al.* 2021).

There is now evidence that populations of *Gyps* vultures have stabilized in both India (Prakash *et al.* 2019, 2024) and Pakistan (Chaudhry *et al.* 2012), while in Nepal, populations of both White-rumped and Slender-billed Vultures have increased rapidly (Galligan *et al.* 2020). The estimated annual rates of increase, 21.7% and 41.3% for these two species, respectively, were significantly higher than the expected maximum population multiplication rate (λ_{max}) for a closed population, estimated using the Demographic Invariants Method (DIM) (Niel & Lebreton 2005), suggesting that at least some of the observed increase in vulture counts in Nepal might be attributable to immigration from India (Galligan *et al.* 2020). The DIM method uses only the age at first reproduction and adult survival probability to estimate λ_{max}, with both parameters assumed to be at values attained under optimal conditions. Neither parameter had then been estimated for vultures in Nepal, so values from stable or increasing populations of related species were used.

Changes in a population trend within a closed population depend on changes in birth and/or death rates, as well as rates of immigration and emigration for open populations (Newton 2008). Monitoring of vulture nesting colonies throughout Nepal has been carried out annually since 2007 (Rana *et al.* 2019). Since 2017, wild White-rumped Vultures in Nepal have been trapped and fitted with Platform Transmitting Terminal (PTT) and Global Positioning System (GPS) transmitters with the aim of estimating survival rates and identifying causes of mortality by recovering carcasses of dead birds (Mallord *et al.* 2024).

The use of supplementary feeding is widespread in the conservation of vultures and condors worldwide (Bildstein 2022). Often the goal is to change the foraging behaviour of birds to reduce their exposure to poisons by providing safe sources of food (Gilbert *et al.* 2007, Cortés-Avizanda *et al.* 2016). There are six 'vulture restaurants' in Nepal, although only one, the Jatayu Restaurant located in Nawalparasi district (hereafter, the Jatayu Restaurant) (Fig. 1), provides food on a regular basis. Such a predictable source of food has the potential to attract large numbers of birds, which could lead to biases in population trend estimates if increases in the number of vultures observed is driven by sightings of birds attracted from far and wide to the supplementary feeding site.

The aims of this study were, first, to update information on vulture population trends in Nepal by adding results from surveys carried out since 2018; secondly, to incorporate values of annual survival probability and breeding productivity into population models; and thirdly, to update the DIM estimate of maximum population growth rate using survival estimates from the study population. By doing this, we aim to assess how much of the increase observed in the population of White-rumped Vultures in Nepal can be attributed to intrinsic demographic processes, rather than immigration, and whether immigration might be associated with access to a predictable food supply at the Jatayu Restaurant.

METHODS

Road transect surveys

Study area

Surveys were conducted in four main regions of the country: Eastern and Western Terai (lowlands) and Western and Far Western Pahad (mid-hills) (Galligan *et al.* 2020). These regions hold most of Nepal's populations of Critically Endangered vultures.

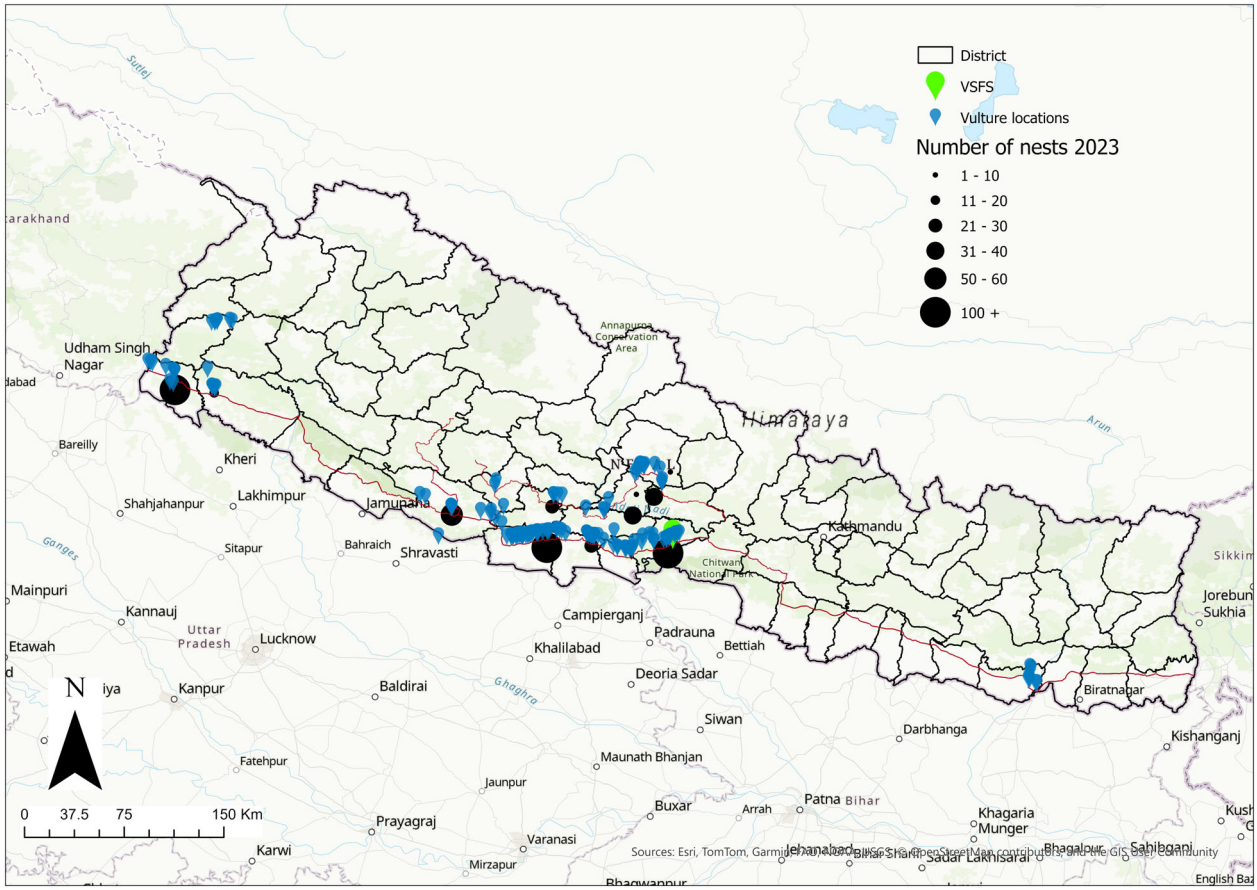

Figure 1. Locations of nesting colonies (black) monitored in 2023 and observations of White-rumped Vultures (blue) on road transect surveys in 2013–2025. The location of the Jatayu Restaurant (Vulture Safe Feeding Site (VSFS), Kawasoti, Nawalparasi District, where vultures were captured to fit with GPS and PTT tags is shown in green.

Sampling design

Surveys were conducted mainly on Nepal's East–West Highway, which runs continuously through the Terai from the eastern to the western border. In addition, arterial roads that run north into the Pahad region were also used. The same roads were used in each of the surveys of a particular region. Surveys were conducted most frequently in the Western Terai, where the majority of Nepal's White-rumped Vultures occur (Rana *et al.* 2019). Regions were surveyed in the same order in each year: Eastern Terai, Western Terai, Far Western Pahad and Western Pahad.

Temporal coverage

Road transect surveys of Nepal's vultures have been conducted between 2002 and 2025, although not in every region in every year (SOM, Table S1).

Field protocols

Surveys were conducted between 0700 and 1700 h, usually in the first 2/3 weeks of May, c. 1 month after the end of the breeding season of White-rumped Vultures, when numbers of this species are highest, after juveniles have fledged, and more birds are active as adults are no longer spending time at a nest. Two surveyors stood on the back of a pick-up truck, which was driven at 20 km/h, scanning for vultures. Once a vulture had been spotted, the truck stopped and the vultures were counted and assigned to species. All perched, flying and soaring vultures were counted, and the locations of each counting stop were recorded with a hand-held GPS device. More details of the study area and methods can be found in Galligan *et al.* (2020).

Nest monitoring

Study area

Monitoring of White-rumped Vulture nesting colonies began in and around the Jatayu Restaurant in Nawalparasi district. Subsequently, the number of nesting colonies monitored has increased across the country annually up to 2025 through opportunistic searching and ground-truthing of locations of GPS-tagged birds (Table S2).

Sampling design

A minimum of three visits were made to view each nest, between October and April. On the first visit (October/November), evidence of nest building was recorded. On the second visit (January/February), the presence of incubating birds and/or nestlings was noted, and on the final visit (March/April), fledging status was assessed. Nests were classified as occupied if any of copulation, courtship behaviour, refurbished nests or the presence of two adults was noted (Bhusal *et al.* 2023). Nests were considered successful if a nestling was known to have fledged.

Temporal coverage

Nest monitoring began in 2007 and has been conducted annually, although none was carried out in 2020 due to travel restrictions imposed during the COVID-19 pandemic.

Field protocols

Monitoring of nests was carried out from prominent vantage points with a telescope, and by walking through the nesting colony.

GPS tagging, tracking and monitoring

Study area

Wild White-rumped Vultures were trapped at the Jatayu Restaurant in Nawalparasi District (Fig. 1). Monitoring and ground-truthing of GPS locations were carried out throughout the country, wherever birds travelled.

Sampling design

A total of 70 wild White-rumped Vultures were trapped in a walk-in aviary (18 × 11 × 6 m), baited with the carcass of an NSAID-free cow or water buffalo. Supplementary cow and buffalo carcasses have been provided at the restaurant frequently (weekly up until 2023; at least monthly thereafter), beginning in 2017 and continuing throughout the period of this study (Mallord *et al.* 2024), allowing monitoring of tagged birds (see below).

Temporal coverage

Trapping occurred on eight dates between April 2017 and March 2023.

Field protocols

We marked each vulture individually, with either two numbered patagial wing tags ($n = 30$; Manufacturer: Maquia Serveis Ambientals, Alicante, Spain) or, after 2020, a single telescope-readable numbered rivetted aluminium leg ring ($n = 40$; I.Ö. Mekaniska AB, Bankeryd, Sweden). Due to wear making identification difficult, five birds had their wing tags replaced with an aluminium ring. We attached a GPS transmitter to each bird, and biometric measurements were taken. Tags were fitted with a thoracic X-strap harness with the tag resting on the bird's dorsal thorax (Orr-Ewing *et al.* 2020). Tags were 30 g Solar Argos/GPS Platform Transmitter Terminal PTTs ($n = 13$; Microwave Telemetry Inc. (MTI), Columbia, MD, USA), 30 g GSM-GPS OrniTrack-30 GPS-GSM transmitters ($n = 55$; Ornitela, Vilnius, Lithuania) or 28 g Telemetry Logger KITE-H LF GPS tags ($n = 2$; Ecotone, Gdynia, Poland). Four birds whose MTI transmitters stopped working were later recaptured and their tags replaced with operational Ornitela tags. MTI tags transmit data via the Argos satellite system, which were accessed via the Collecte Localisation Satellites (CLS) Argos website (https://argos-system.clsamerica.com), while data transmitted from Ornitela/Ecotone GPS-GSM tags were obtained via mobile phone connection, and accessed from the manufacturers' websites. The maximum combined weight of the transmitter, harness, wing tags or rings was 110 g and constituted about 2.3% of body-weight. Birds were released immediately after tagging.

We checked vultures feeding at the restaurant to read wing tags and rings opportunistically. We monitored the data from the transmitters daily. If GPS fixes suggested the bird was consistently stationary, or if accompanying accelerometer/battery voltage/temperature data suggested that the bird might have died, we travelled to the location and searched for it. Carcasses of dead birds were retrieved and, if not too decomposed, underwent post-mortem examination.

Statistical analysis

All modelling was conducted in R, version 4.5.0 (R Core Team 2025).

Road transect surveys

Following the methods of Galligan *et al.* (2020), we used two model structures to describe changes over time in the population index during the whole period of the study (2002–2025). First, we fitted quasi-Poisson models using the function *'glm'* in R using the raw count data, which includes 44 counts in four regions in 19 years (SOM, Table S3). The count of vultures in a given year and region was the dependent variable, and year and region were both modelled as categorical fixed effects. We fitted a quasi-Poisson model to account for overdispersion in the count data. This produces proportional changes between years in population size, which were assumed to be the same across all regions. The model has a logarithmic link function, so the vulture count C_{ij} in region i and year j is modelled as:

$$C_{ij} = \exp\left(k_i + p_j\right),$$

where C_{ij} is the count for the jth transect in the ith year. Region effects are represented by the fitted regression coefficients p_j. The coefficients k_i represent the year effects and are the logarithms of the abundance of vultures in the ith year, allowing for region effects, expressed as a proportion of the abundance of vultures in the first year of the series in the study period (2002). Hence, $\exp(k_i)$ provides an index of population density in the ith year, relative to that in the first survey of the series.

Inspection of a graph of $\exp(k_i)$ plotted against year (Fig. 2) indicated an abrupt change in population trend during the study period, as was also observed for both White-rumped and Slender-billed Vultures in Nepal by Galligan *et al.* (2020). We therefore fitted a similar model to that described above, but with year t modelled as a continuous variable, using piecewise quasi-Poisson regression, but assuming that the population showed two different log-linear trends during the study period, with the trend slope changing at a particular date: the breakpoint date t^*. The fitted model was:

$$\log_e(C_{ij}) = p_j + b_1{}^* t + b_2{}^* (t - t^*),$$

where p_j are the fitted region effects, b_1 and b_2 are regression coefficients and $(t - t^*)$ is the difference between times t and t^*, but with $(t - t^*)$ set to zero when $t<t^*$. We found the optimal value of t^* at which the residual deviance was minimized by using an iterative bisection search (Kalbfleisch 1979). The population multiplication rate in the years before the breakpoint date was estimated as $\lambda_{\text{pre}} = \exp(b_1)$ and in the years after the breakpoint date by $\lambda_{\text{post}} = \exp\ (b_1 + b_2)$. We obtained 95% confidence intervals (CIs) for the estimates of λ_{pre}, λ_{post} and t^* by a bootstrap method. We drew a sample of 44 region–year-specific counts at random and with replacement from the 44 actual counts. We then fitted the piecewise regression model to this sample, as described above, and saved the resulting values of λ_{pre}, λ_{post} and t^*. We repeated this procedure 10 000 times, ranked the bootstrap estimates and took the bounds of the central 9500 values as the CIs.

We conducted an additional analysis of the road transect data to test whether geographical variation in population trend over time within Nepal after the breakpoint date was related to proximity to the Jatayu Restaurant. First, the road transect route was divided into 10-km sections, and the distance from the centre of each section to the restaurant was measured. Secondly, all vulture sightings during the

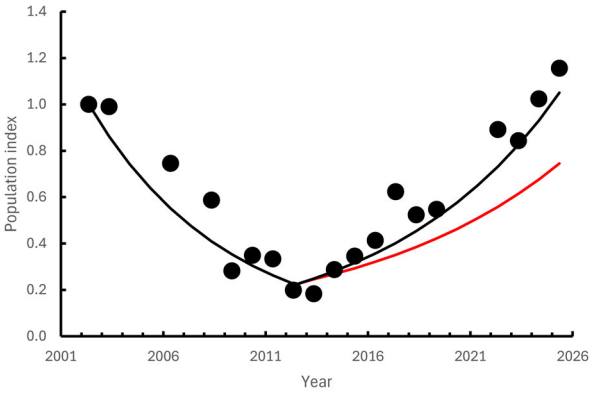

Figure 2. Annual population index values (circles) for White-rumped Vultures in Nepal for 2002–2025 derived from a quasi-Poisson model with effects of region and year as categorical variables. The index is population relative to that in 2002. The black curve shows expected index values from a piecewise regression model. The red curve shows results from a simulation model of the population based upon demographic rate estimates, which assume that breeding productivity increased over time and that population age structure was not stable (see Supplementary Information). However, results from the LMM described in the main text, which assumes constant productivity and stable age structure, are virtually indistinguishable from the red curve.

period of recovery (2013–2025) were assigned to the nearest 10-km section. We modelled the number of vultures recorded during road transect surveys in each section (including zero counts) as the dependent variable with a log-link function and a quasi-Poisson error distribution. The independent variables were year as a continuous variable and the distance from the 10-km section to the Jatayu Restaurant. We included the two-way interaction between year and distance in the model. We used a *t*-test on this two-way interaction term to determine whether geographical variation in population changes during the period of recovery was related to distance from the Jatayu Restaurant. If vulture numbers had increased more rapidly over time near the Jatayu Restaurant during the recovery because birds were increasingly being attracted to it by the supplementary food or presence of other vultures, we expected this interaction to be negative—that is a slower rate of increase at greater distance from the restaurant.

Nest success

The total number of nests monitored per year increased over time because of an increase in survey effort, so we did not attempt to model nest numbers in relation to time as a measure of population change. Annual productivity (fledglings per nest) was modelled using logistic regression with a binomial error function and logit link function. Annual productivity is equivalent to the proportion of nests that are successful for *Gyps* vultures because they only lay one egg per clutch. The binary dependent variable was the number of successful nests, as a proportion of the total monitored, with the outcome of each nest being modelled as if it were the result of a binomial trial. The effect of year was modelled as a continuous covariate to estimate trend over time. We repeated this analysis for the whole study period (2007–2025), and separately for the period of population recovery (2013–2025). We calculated 95% binomial CIs (Clopper & Pearson 1934) for the annual estimates of nest success.

Survival of GPS-tagged White-rumped Vultures

We assumed that a bird whose tag had stopped transmitting and which was not subsequently seen alive had died at the time when the tag was lost to follow-up, even if the bird's carcass was never located (Mallord *et al.* 2024). This is a 'worst case' assumption, in that it is possible that some events we took to represent deaths might have been due to either the failure of the transmitter or shedding of the tag and harness, with the bird not being recorded subsequently by direct observation of the ring or wing tag. If a bird's tag stopped working, but it *was* subsequently seen alive, it was assumed to have been alive and monitored up to the last day on which data transmissions were received. The data were right-censored at that date ($n = 15$ birds). For those four birds that were recaptured and fitted with a working transmitter after their tag ceased to provide data, the period of monitoring re-started. We based our estimates of the probable date of death on changes in accelerometer data and the reduction in battery voltage and temperature of the tag, using data provided by the tag manufacturers.

A total of 25 birds were tagged as subadults, defined as being between 1 and 4 years old. Some of these birds would have become adults during the monitoring period. Therefore, for the purpose of assigning the number of days over which the birds were monitored to either adult or subadult classes, each bird was assigned at random to one of three calendar age-classes at release (assuming an age at first breeding of 4 years), with equal probability of being assigned to each class. The calendar age-classes were 1/2, 2/3 and 3/4 years old, under the assumption that birds become adult at 4 years old. For birds of 3/4 years old, a maximum of 365 days would be assigned to the subadult class, that is, until the birds become adult, after which the remaining days during which it was monitored were assigned to the adult class. For birds 2/3 and 1/2 years old, a maximum of 730 and 1095 days (365×2 and 3, respectively) were assigned to the subadult class, respectively, and the remaining days to the adult class. This process was repeated assuming an age of first breeding of 3 and 5 years; hence, survival estimates differed among the three cases.

We calculated daily mortality rate (DMR) as m/d, where m is the number of deaths and d is the number of bird-days over which birds were monitored. We calculated annual survival rates (S) from the DMRs as:

$$S = (1 - \mathrm{DMR})^{365.25}.$$

We calculated Clopper–Pearson exact binomial 95% confidence limits (CLs) for DMR (Clopper & Pearson 1934) and used these limits to calculate CLs for S using the expression above. Some surviving birds continued to be monitored at the time

of analysis, which was 26 August 2025. We right-censored the data for these surviving birds at that date so that their days of monitoring were included in the analysis but without death having been observed. Differences between adult and subadult annual survival rates were compared using a Fisher exact 2×2 test, using m and $(d - m)$ values for each of the two groups as the entries in a 2×2 contingency table.

Population modelling

As White-rumped Vultures go through 2–4 years as a subadult, we estimated the intrinsic rate of population increase (λ) by use of an age-dependent Leslie matrix model (LMM; Leslie 1945), as follows (example given for age at first breeding of 4 years):

$$A = \begin{bmatrix} & & & & P \\ S0 & & & & \\ & S1 & & & \\ & & S2 & & \\ & & & S3 & S4 \end{bmatrix} * \begin{bmatrix} N\,juv \\ N\,SA\,1 \\ N\;\;SA\,2 \\ N\,SA\,3 \\ N\,Ad \end{bmatrix}$$

where *S0* is survival from fledging to 1 year old (1st year), *S1-3* are values for subadult (1, 2 and 3 years old) and *S4* is for adults (age 4 years or more). Values for *S1* to *S4* were estimated from the monitoring data from tagged vultures. We assumed subadult survival rates *S1* to *S3* to be the same at each year of age. This was a necessary assumption because tagged subadult birds could not be aged more precisely at capture, except to say that they were not juveniles and not adults. The model is for females only. Tagged birds were not sexed and we assumed that annual survival rates were the same for males and females. *P* is an estimate of annual productivity, derived from monitoring of nesting colonies throughout Nepal. This figure was divided by 2 to reflect that this is a female-only matrix model (Beissinger *et al.* 2006). As there are no estimates of survival of White-rumped Vultures in their first year of life, we used an estimate of juvenile survival (*S0*) from another *Gyps* species, the Griffon Vulture *G. fulvus* in France (Chantepie *et al.* 2016). This value, 0.65 (95% CI; 0.53–0.77), was similar to that obtained for Cape Vultures *G. coprotheres* in South Africa after the introduction of supplementary feeding (0.69; Piper *et al.* 1999). Little is known about the maximum lifespan of White-rumped Vultures in the wild. The maximum recorded longevity for a bird in captivity is 17 years, 2 months (Flower 1938) and the record for the closely related White-backed Vulture *G. africanus* in the wild is 19 years, 1 month (Paijmans *et al.* 2017). Therefore, the matrix model was run for 20 generations to estimate the intrinsic rate of increase during the recovery period (λ_{post}) and the stable age distribution of the population. We calculated a 95% CI for λ_{post} using the package 'mpmsim' (Jones 2025), which uses parametric bootstrapping, taking 1000 random independent draws using the sampling distribution of each underlying transition rate, with the following sample sizes: $n = 356$ nests (average number of nests, 2007–2025); $n = 245$ juveniles (average number of nests multiplied by average productivity); $n = 25$ subadults and $n = 45$ adults GPS-tagged (see above). The relative impact of the precision of each demographic parameter on the precision of the λ estimate was estimated by running the matrix model using the lower and upper 95% CIs for each parameter in turn. The population matrix was also run assuming an age at first breeding of 3 and 5 years. Analysis of matrix population models was carried out in the R package 'popbio' (Stubben & Milligan 2007).

Our results indicated that two of the assumptions underlying these LMM calculations were not met: (1) we assumed that productivity *P* was constant but our analysis showed that *P* increased progressively during the recovery period; (2) we estimated λ_{post} after a stable age structure had been attained, but we expected the proportions of the different age-classes to change during the transition from population decline to recovery. To check for possible effects of these failures of assumptions on the results from the LMM analysis, we constructed a detailed simulation model, which is described in the supplementary information (SOM, S4). We used this model to obtain alternative values for λ_{post} for a model with $\alpha = 4$ years.

Maximum population multiplication rate

We estimated the maximum population multiplication rate (λ_{max}) using the DIM (Niel & Lebreton 2005). The only data required for this are estimates of the annual survival rate of adults, which we took from the monitoring of GPS-tagged birds, and the age at first breeding. We then inserted these values into equation 15 (appropriate for long-lived

species) from Niel and Lebreton (2005) to estimate λ_{max}. We calculated 95% CIs by using the 95% CIs of the adult survival estimate. Following Galligan *et al.* (2020), we estimated λ_{max} using values of age of first breeding of both 4 and 5 years of age, taken from the related Griffon Vulture (Cramp & Simmons 1980, Ferrière *et al.* 1996), and 3 years from Cape Vultures (Monadjem *et al.* 2014).

RESULTS

Road transect surveys

With 'year' modelled as a categorical variable, the dispersion parameter θ of the quasi-Poisson model was 4.88. When plotted against time, the annual population index values from this model indicated a tendency to decline from 2002 until about 2012 and to increase thereafter until 2025 (Fig. 2).

With 'year' modelled as a continuous variable and assuming that the midpoint of road transect survey dates was on the mean survey date in all years (10 May), a breakpoint in the population trend was estimated to have occurred in 2012 (9 June 2012, 95% CI: 6 August 2011 to 14 April 2013). In the period before the breakpoint (2002–2012), the estimated mean population multiplication rate λ_{pre} was 0.862 (annual decline of 13.8% per year) with 95% CLs of 0.842–0.881. In the period after the breakpoint (2013–2025), the estimated mean population multiplication rate λ_{post} was 1.127 (annual increase of 12.7% per year) with 95% CLs of 1.106–1.148.

We modelled counts of vultures in 10-km road transect sections during the period of recovery (2013–2025) in relation to 'year', modelled as a continuous variable, distance of the road section from the Jatayu Restaurant and their two-way interaction. The dispersion parameter θ of the quasi-Poisson model was 27.18. The interaction term between distance and year was positive (0.00043), which is the opposite of our expectation under the hypothesis that vultures increased more rapidly in areas near to the Jatayu Restaurant than they did in more distant areas. The interaction term was not significantly different from zero ($t = 0.91$, $P = 0.36$).

Nest monitoring

A total of 6410 nests were monitored between 2007 and 2025 (Table S2), an average of 356 per year. The number of nests monitored per year increased over time, but this trend is due largely to changes in survey effort and therefore cannot be used to estimate population trends. Average productivity (the proportion of successful nests) was 0.692 (95% CI: 0.644–0.740). However, there was a significant positive trend over time in productivity across the whole study period (2002–2025). The fitted logistic regression model was logit (proportion successful) $= -56.26 + 0.02827 \times$ calendar year. The regression coefficient was significantly different from zero ($t_{16} = 5.33$; $P < 0.001$; Fig. 3). The trend in productivity was also positive and statistically significant if the analysis was restricted to the period of population increase (2013–2025) ($t_{10} = 2.93$; $P = 0.015$).

Survival estimates

Under the assumption that subadults become adult at 4 years old, tagged adult White-rumped Vultures were monitored for a total of 74 368 bird-days and 11 deaths of adults were observed. Tagged subadults were monitored for 15 997 bird-days during which two deaths were observed. This gave estimated annual survival rates of 0.947 (95% CI 0.912–0.977) for adults and 0.955 (0.829–0.987) for subadults. Equivalent results for age of first breeding of 3 and 5 years are shown in Table 1. There was no significant difference between the rates for the two age-classes assuming an age of

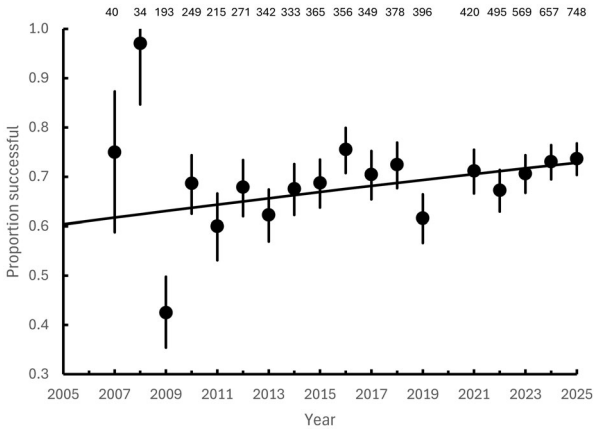

Figure 3. Proportion of nests of White-rumped Vultures in Nepal that were successful in relation to year 2007–2025. Vertical lines are Clopper–Pearson 95% confidence intervals of the annual estimates. The curve shows the fitted logistic regression model. Numerals at the top of the Figure show the numbers of nests monitored in each year.

Table 1. The number of days over which adult and subadult GPS-tagged White-rumped Vultures were monitored, along with estimates of annual survival with lower and upper confidence limits (LCL, UCL, for ages of adulthood of 3, 4 and 5 years).

Age of adulthood	Days Adult	Deaths	*S*	LCL	UCL	Days Subadult	Deaths	*S*	LCL	UCL
3	77 432	11	0.949	0.911	0.974	12 933	2	0.945	0.815	0.993
4	74 368	11	0.947	0.912	0.977	15 997	2	0.955	0.829	0.987
5	71 031	10	0.950	0.910	0.976	19 334	3	0.945	0.847	0.988

adulthood of 3, 4 or 5 years (Fisher Exact Test, $P > 0.7$ in all cases).

Population modelling

We initiated the initial model population with 100 adults. Based on mean annual nesting success (see above), this population would fledge 34.6 juveniles. Based on the annual juvenile survival rate of Griffon Vulture (0.65, Chantepie *et al.* 2016) and subadult survival (0.955, see above), this would give 64.5 subadults in the three subadult age-classes combined. This gave a total population of 199.1 birds.

$$A = \begin{bmatrix} 0 & 0 & 0 & 0 & 0.346 \\ 0.65 & 0 & 0 & 0 & 0 \\ 0 & 0.955 & 0 & 0 & 0 \\ 0 & 0 & 0.955 & 0 & 0 \\ 0 & 0 & 0 & 0.955 & 0.947 \end{bmatrix} * \begin{bmatrix} 34.6 \\ 22.5 \\ 21.5 \\ 20.5 \\ 100 \end{bmatrix}$$

For an age of first breeding of 4 years, after 20 generations, the intrinsic rate of increase for the recovery phase, λ_{post}, was 1.087 (8.7% increase per annum), with 95% CLs of 1.033 and 1.127. The stable age distribution consisted of 17.4% juveniles, 27.9% across the three subadult classes and 54.7% adults. A similar result was obtained when population matrices were run with demographic rates set at upper and lower 95% confidence levels, with greater differences in λ_{post} when adult survival rates were changed compared with the other demographic parameters (Table 2). Values of λ_{post} for age at first breeding of 3 and 5 years are shown in Table 3.

We used a simulation model (SOM, S4) with α set to 4 years to check whether the results obtained from the LMM with constant productivity and stable age structure were affected if productivity was instead assumed to change over time, as our analysis of nest success indicated it had, and if age structure changed, as we expected given that demographic parameters are likely to

Table 2. Effect of the precision of estimates of demographic rates on the population multiplication rate during population recovery (λ_{post}) of White-rumped Vultures in Nepal estimated using a Leslie Matrix Model with constant parameter values and stable age structure. Age at first breeding α was assumed to be 3, 4 or 5 years. Lower (lower confidence limit (LCL)) and upper (upper confidence limit (UCL)) values of λ were obtained with each of the demographic parameters in turn set at its lower or upper 95% confidence limit and all other parameters set to their best estimate values.

	$\alpha = 3$ years ($\lambda_{post} = 1.099$)		$\alpha = 4$ years ($\lambda = 1.087$)		$\alpha = 5$ years ($\lambda = 1.075$)	
Demographic parameter altered	LCL λ	UCL λ	LCL λ	UCL λ	LCL λ	UCL λ
Juv S	1.079	1.119	1.070	1.103	1.060	1.089
SA1 *S*	1.085	1.105	1.074	1.090	1.066	1.079
SA2 *S*	1.085	1.105	1.074	1.090	1.066	1.079
SA3 *S*			1.075	1.090	1.066	1.079
SA4 *S*					1.066	1.079
Ad *S*	1.073	1.118	1.065	1.107	1.050	1.092
P	1.092	1.107	1.081	1.094	1.069	1.080

Table 3. Mean annual population multiplication rate λ_{post} of White-rumped Vultures in Nepal, estimated from road transect counts for the recent period of increase (2013–2025), compared with the value of λ_{post} estimated using a Leslie Matrix Model (LMM) with constant demographic rates estimated for 2013–2025 and an assumed age at first breeding of $\alpha = 3$, 4 or 5 years. Also shown are expected maximum population multiplication rates λ_{max} calculated by the Demographic Invariants Method (DIM) from the mean annual survival rate for adults and the same three alternative values of the age at first breeding α.

Species	λ	95% LCL	95% UCL
Road transects	1.127	1.107	1.148
LMM ($\alpha = 3$ years)	1.099	1.041	1.146
LMM ($\alpha = 4$ years)	1.087	1.033	1.127
LMM ($\alpha = 5$ years)	1.075	1.023	1.116
DIM ($\alpha = 3$ years)	1.116	1.080	1.144
DIM ($\alpha = 4$ years)	1.097	1.068	1.119
DIM ($\alpha = 5$ years)	1.084	1.059	1.102

have changed at the transition between decline and recovery. Using the simulation model with a trend in productivity and changing age structure we found that λ_{post} for 2013–2025 was 1.098, which is only slightly different from the value for the LMM with α set to 4 years ($\lambda_{post} = 1.087$). This model gave the results shown by the red curve in Figure 2. We forced the simulated population to decline before the recovery began at the same rate as that estimated from our analysis of the road transect surveys. We did this by assuming that the annual mortality rates before the recovery began were as they were during the recovery, except that there was an additional mortality rate imposed on all age-classes. We determined the additional mortality rate required iteratively and found that a rate of 0.206 was required, that is 20.6% of birds dying per year because of a factor not operating from 2013 onwards.

The value of first-year survival rate *S0* used in the LMM and in the simulation model was taken from a study of another species in a different country (Griffon Vulture in France), so we altered the value of *S0* until the modelled λ_{post} for 2013–2025 matched that estimated using the road transect data ($\lambda_{post} = 1.127$). The required value of *S*0 was 0.849. This is considerably higher than the upper 95% CL for the estimate of *S0* for Griffon Vulture in France (0.77) though lower than the value of subadult survival we estimated for the recovery period (0.955). The equivalent value for *S0* required to give $\lambda_{post} = 1.127$ calculated using the simulation model was 0.842.

For an age of first breeding of 4 years and adult survival probability of 0.947, the estimate of λ_{max} calculated using the DIM was 1.097 (i.e. a 9.7% rate of annual increase), with 95% CLs of 1.068 and 1.119. Values for λ_{max} for age of first breeding of 3 and 5 years of age are shown in Table 3. Our results suggest that the observed rate of population growth during the recovery period, based on the road transect data, may have been somewhat more rapid than expected from the demographic rates estimated during the recovery based on the LMM, simulation model and DIM calculations. However, the CIs of the estimates of λ obtained by the different methods overlap (Table 3).

DISCUSSION

Recent road transect surveys have shown that the population of White-rumped Vultures in Nepal has continued to increase since 2012–2013 and that annual survival rates of adults and subadults during this period were high. Sensitivity analysis showed that the demographic parameter that most strongly influenced population multiplication rate was the annual survival rate of adults. Similarity between the intrinsic rate of increase estimated from the matrix population model, the simulation model and the DIM, and that from survey counts suggests that the population increase can be largely explained by intrinsic demographic processes, such as high survival and productivity, and that immigration from neighbouring India has probably played a minor role, if any. That the recovery only began after the removal of diclofenac provides further circumstantial evidence, not that it is needed given the wealth of other evidence, of the central role of the drug in the historical declines of *Gyps* vultures in the region.

Populations of White-rumped Vultures in Nepal declined until around 2012–2013 (Galligan *et al.* 2020). The subsequent recovery is associated with the high estimated annual survival rates reported here of wild GPS-tagged White-rumped Vultures, which is probably due to the removal of diclofenac from veterinary pharmacies in the country (Galligan *et al.* 2021). Like other large raptors, vultures are long-lived birds (Sæther 1989, Newton *et al.* 2016), with published annual survival estimates for *Gyps* species of around 90% (Sarrazin *et al.* 1994, Monadjem *et al.* 2012, Arrondo *et al.* 2020). Although conservative (i.e. potential tag loss is treated as mortality), our survival estimates for White-rumped Vultures—94.7% for adults and 95.5% for immatures—are comparably high. Both breeding productivity and immature survival rates were higher in our study than in some other populations of *Gyps* vultures (Sarrazin *et al.* 1994, Xirouchakis 2010). This suggests that these demographic rates may be elevated because the population has not yet recovered sufficiently to be close to its equilibrium size, at which density-dependent competition and behavioural interference may depress these rates (Fernandez *et al.* 1998). It is plausible that the survival rate of juveniles *S0* was also higher than is typical because it was not depressed by effects of high population density. Hence, the value of *S0* required to make λ_{post} match that estimated from the road transect data (0.842–0.849) may apply in this population. Diclofenac caused such high mortality that White-rumped Vultures declined across South Asia by

~50% per annum (Green *et al.* 2004). The high survival rates in Nepal suggest that birds have not been strongly affected by NSAID poisoning or any other anthropogenic causes of mortality, such as poison baits, electrocution and collision associated with energy infrastructure during the recovery (Mallord *et al.* 2024). Adult survival was the demographic parameter that contributed most to the population growth rate, which is consistent with other long-lived species with low fecundity (Sæther & Bakke 2000).

Immigration of vultures from India could have contributed to the rapid increase in the population index of White-rumped Vultures in Nepal. GPS tracking has confirmed that White-rumped Vultures in Nepal regularly travel to and from India (Mallord *et al.* 2024). The matrix model, simulation model and DIM ($\lambda = 4$) suggest that the population should have increased by a factor of between 2.7 and 3.9 between 2013 and 2025, while analysis of the road transect survey data estimated a 4.2-fold increase. However, the CIs of the estimates of population multiplication rate from the recovery period overlap, so there is no conclusive evidence for immigration.

Although the number of vultures attracted to supplementary food at the Jatayu Restaurant has increased over the survey period (maximum count of 393 White-rumped Vultures in February 2023; BCN unpubl.), our modelling indicates that proximity to the restaurant has not driven changes in the number of vultures recorded across the country. If immigration has occurred, a more plausible explanation is that Indian birds have simply been attracted by the higher overall density of locally bred wild vultures in Nepal. Vultures are social animals and their ability to find food is socially facilitated (Houston 1979, Jackson *et al.* 2008). Once λ in Nepal exceeded 1 because diclofenac disappeared, attracted birds may have accelerated the growth rate further.

The rapid increase in populations of White-rumped and Slender-billed Vultures in Nepal contrasts with the situation in India. Although populations of *Gyps* vultures have remained stable in India since the ban on veterinary use of diclofenac (in 2006), there has been no sign of a recovery (Prakash *et al.* 2019, 2024). This may be due to differences in the availability of diclofenac. Unlike Nepal, which was declared diclofenac-free in 2023 (Pandey 2023), the drug is still widely available in India, including some in illegally manufactured large multi-dose vials (Mallord *et al.* 2025). While a recovery in vulture numbers may be expected in areas where diclofenac has been eradicated, it is possible that emigration to Nepal has masked some population recovery in neighbouring parts of India. However, other vulture-toxic drugs such as aceclofenac, ketoprofen and nimesulide have also been widely available. These drugs have only recently been banned (SAVE 2023, 2025), so their use may have prevented population recovery.

Although the continuing recovery is positive, populations are still at very low levels compared with before the onset of the declines in the mid-1990s, and are still at a high risk of extinction (Birdlife International 2021). Although sales of diclofenac for veterinary use have been reduced to zero in Nepal (Galligan *et al.* 2021), other vulture-toxic NSAIDs, for example nimesulide (Galligan *et al.* 2022), are still available. There is also a risk that, without stringent safety testing of new drugs on vultures, other toxic drugs could be approved that have similar catastrophic effects to diclofenac on vulture populations (Cook *et al.* 2024). Actions to ban vulture-toxic NSAIDs that are already available, and to put in place regulations requiring the safety testing to vultures of new drugs prior to licensing should be prioritized, as recommended by a Resolution by the Convention on Migratory Species (Convention on Migratory Species 2020). Urgent implementation of these actions is needed to prevent the roll-back of the conservation successes already achieved.

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AUTHOR CONTRIBUTIONS

John W. Mallord: Conceptualization; methodology; writing – review and editing; writing – original draft; formal analysis. **Ishwari P. Chaudhary:** Investigation; writing – review and editing. **Rhys E. Green:** Conceptualization; methodology; software;

formal analysis; supervision; writing – original draft; writing – review and editing. **Deelip C. Thakur:** Investigation; writing – review and editing. **Deu B. Rana:** Investigation; writing – review and editing. **Ankit B. Joshi:** Methodology; writing – review and editing; investigation; supervision; data curation. **Bed Kumar Dhakal:** Writing – review and editing; investigation. **Toby H. Galligan:** Conceptualization; supervision; methodology; writing – review and editing; project administration. **Krishna P. Bhusal:** Supervision; investigation; data curation; methodology; writing – review and editing. **Ishana Thapa:** Investigation; writing – review and editing; methodology; conceptualization; data curation; supervision; resources.

ETHICAL NOTE

None.

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CONFLICT OF INTEREST STATEMENT

The authors have no conflicts of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available on request from the corresponding author. The data are not publicly available due to privacy or ethical restrictions.

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SUPPORTING INFORMATION

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

Table S1. Regions covered (✓) during road transect surveys in Nepal between 2002 and 2025.

Table S2. Total number of monitored and successful White-rumped Vulture nests and percentage success, in lowland Nepal between 2007 and 2025. *Monitoring was not possible in 2020 due to travel restrictions associated with the COVID-19 pandemic.

Table S3. Counts of White-rumped Vultures in 2002–2023 on road transect surveys in four regions of Nepal.