

Breeding ecology of critically endangered Long-billed vulture *Gyps indicus* (Scopoli, 1786) and White-rumped vulture *G. bengalensis* (Gmelin, 1788) in Kaghaznagar Forest Division and its adjoining areas in the Deccan Plateau, India

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Abstract

Gyps species declined rapidly between the late 1990s and early 2000s in southern Asia due to the use of diclofenac and are listed as Critically Endangered species. Long-term data on breeding ecology is essential to understand the population trends of these threatened species. This study assessed the breeding phenology and reproductive performance of two critically endangered *Gyps* species—Long-billed *Gyps indicus* (Scopoli) (LBV) and White-rumped *Gyps bengalensis* (Gmelin) (WRV) vultures—through long-term monitoring at breeding colonies in Kaghaznagar and Sironcha Forest Divisions in the Deccan Plateau of India between 2010 and 2021. LBV began their nest construction and copulation in the second week of October, and ended in the fourth week of November, while the WRV completed the same between the first and second weeks of October. LBV started egg-laying during the first week of December and ended in the first week of January, with a peak during the third week on 14 December, and the mean incubation period was 54±1 days. The WRV completed their egg-laying early, during the second and third weeks of October, and peaked during the second week on 14 October and had a relatively longer incubation of 61±1 days. For LBV, hatching peaked during the first week of February, and the mean nestling period was 103±2 days, while for WRV hatching peaked much earlier, during the third week of December and the mean nestling period was 105±1 days. Overall nest success, breeding success, and productivity estimated based on 159 breeding pairs of LBV observed over 12 years were lower compared to that of 124 breeding pairs of WRV observed over 6-year period. The decline in breeding success of LBV since 2019 is discussed in light of cattle poisoning reported in 2018, and the reopening of the Sirpur paper industry (Kaghaznagar) in 2017 that discharges its hazardous effluent into the Peddavagu stream. Therefore, the present study suggests long-term monitoring of breeding colonies including evaluation of the drivers of population and breeding, molecular and toxicological studies, and implementation of Vulture Safe Zones to save these critically endangered *Gyps* vultures from local extinction.

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Introduction

Vultures are the only group of obligatory vertebrate scavengers inhabiting diverse biomes from rain forests of Amazon to the East African Savannah to the Sahara Deserts and high Himalayas (Ruxton and Houston, 2004; Buechley and Sekercioglu, 2016). They exclusively feed on dead and decaying vertebrate carcasses (Ali and Ripley, 1968; Mundy et al., 1992), thereby keeping the environment clean and healthy and preventing the spread of diseases that affect mammals, including humans (Iqbal et al., 2011). Their bare featherless neck, broad wings, keen vision, and highly acidic stomachs are the evolutionary advantages of scavenging (Coleman and Fraser, 1989). There are twenty-three species of vultures in the world; India harbors nine of them, of which southern India is home to three—Long-billed vulture *Gyps indicus* (Scopoli, 1786), White-rumped vulture *G. bengalensis* (Gmelin, 1788), and Egyptian vulture *Neophron percnopterus* (Linnaeus, 1758) (MoEF, 2006). Recent scholarship on the Indian vultures has time and again highlighted the importance of effective conservation of these endangered scavenging birds that act as an index of ecosystem health (Markandya et al., 2008; Cuthbert et al., 2011; Kanaujia and Kushwaha, 2013; Prakash et al., 2019).

Long-billed vulture *Gyps indicus* (hereafter referred to as LBV) is a colonial cliff-nesting raptor that breeds in the southeast of Pakistan and in peninsular India, south of the Gangetic plain, east through Madhya Pradesh, north to Nilgiris, and occasionally further south (Collar et al., 2001). On the other hand, the White-rumped vulture *G. bengalensis* (hereafter referred to as WRV) is a colonial tree-nesting raptor that breeds in Pakistan, India, Nepal, Bhutan, Myanmar, Thailand, Laos, Cambodia, and southern Vietnam, and may be extinct in southern China and Malaysia (Collar et al., 2001). Earlier studies on LBV and WRV in India show that their populations have declined by over 92% between 1991 and 2000 (Prakash et al., 2003, 2005). Repeated surveys have shown that the annual decline was at an alarming rate of 48% for WRV and 22% for LBV between 2000 and 2003 (Green et al., 2004). The decline of these species is attributed to the rampant use of diclofenac, an anti-inflammatory drug widely used for cattle (Shultz et al., 2004). As a result, these *Gyps* species have been listed under the ‘Critically Endangered’ category by the International Union of Conservation of Nature (Birdlife International, 2021), and are listed under Schedule I of the Indian Wildlife (Protection) Act 1972. Worldwide, 78% of vulture species are currently threatened by accidental and deliberate abuse of pesticides (Plaza et al., 2019).

Vultures are long-living species, sexually mature at the age of five, and have a prolonged breeding cycle with several phases, viz., copulation and nest construction, egg-laying, incubation, nestling stage, and fledgling stage. Clutch size is one (Grubb, 1983)

and there may occasionally be a second when the first egg is broken within a short period of laying (Clark, 1994). Both sexes contribute to all aspects of breeding including nest construction, territorial defense, incubation, and rearing young. Both LBV and WRV breed in colonies of up to 20 breeding pairs, with LBV using mostly cliff ledges, while WRV uses the taller trees for nesting (Newton, 1979; Naoroji, 2006). Many earlier studies on vultures also reported the continuous use of the same nesting site for many years (Rasmussen and Anderton, 2005; Davit, 2009; Kushwaha et al., 2009; Kanaujia et al., 2010; Vergara et al., 2010). Despite their declining status, since 2000, long-term studies on breeding ecology, an essential aspect to understand their reproductive performance in recent years, are still rare on WRV (Gill, 1921; Thakur, 2015; Samson and Ramakrishnan, 2020) and LBV (Kulshreshtha, 2001; Rasmussen and Anderton, 2005; Naoroji, 2007; Kushwaha et al., 2009; Kanaujia et al., 2013; Khatri, 2015; McClure et al., 2021). In this paper, we present long-term data collected from 2010 to 2021 on the breeding ecology, which includes breeding phenology and reproductive performance of Long-billed vulture and White-rumped vulture from Kaghaznagar Forest Division and its adjoining areas in the Deccan Plateau, India. The breeding phenology covered in this paper includes (i) nest-construction and copulation, (ii) egg-laying, (iii) incubation, (iv) hatching, and (v) fledgling periods, and the reproductive performance includes (i) hatching, (ii) fledgling, (iii) breeding, and (iv) productivity.

Material and Methods

Study area

The Kaghaznagar Forest Division lies in Kumrambheem Asifabad District in Telangana state, India. The two species of vultures are found along the Pranahita River in this division. The forest division is spread across 900 km² and acts as a corridor for three tiger reserves: Kawal Tiger Reserve, northern region, which is connected to the Tadoba Andhari Tiger Reserve of Maharashtra, and in the east to the Indravati Tiger Reserve of Chhattisgarh, and the northwest stretch is connected to Tipheshwar Wildlife Sanctuary in Maharashtra. With respect to climatic conditions, the area has three distinct seasons: summer, monsoon, and winter. During summer, the temperature varies between 35 °C and 42 °C. The monsoon season begins with the onset of the southwest monsoon during the second week of June, and lasts till the end of October, with an average rainfall of 1,000 mm. The winter season commences by the end of November and continues up to February with temperatures between 10 °C and 15 °C. The Pranahita River is perennial and acts as the main water source for wildlife; it flows along the southern boundary of the range. Finally, the Peddavagu stream flows in these forests and tributes into the Pranahita River, after crossing the Palarapu Cliff.

Study Site I: Palarapu Cliff (Fig. 1)

Palarapu Cliff (19°12'46.38" N, 79°54'48.72" E; 211 m elevation), in which the first natural breeding colony of LBV was observed, is located in the Bejjur Reserved Forest, and is a part of Kaghaznagar Forest Division, adjoining Nandigaon village, at the confluence of Peddavaagu stream and Pranahita River. Its southern face is 75 m high elevated rock cliff (108 m, total height of the cliff). The study area is bordered by a linear stretch of agricultural fields, which extend up to the Pranahita River, and further by the natural habitats of Sironcha Forest Division in the state of Maharashtra on the east, Bejjur Reserved Forest, Kaghaznagar Forest Division on the west and north, and by Peddavagu stream on the south by the natural habitats of Bellampalli Forest Division, Telangana.

Study Site II: Lakkameda Cliff

Lakkameda Cliff (19°10'45.00" N, 80°6'38.00" E; 592 m elevation), where the second natural breeding colony of LBV was observed, is located about 10 km east of Palarapu Cliff in the Pranahita Range, Sironcha Forest Division, Maharashtra. The northern side of the cliff is bordered by Pranahita Wildlife Sanctuary and Kolamarka Conservation Reserve bordering the southern side. Its eastern and western sides are covered by the natural habitats of Sironcha Forest Division, Maharashtra. The Indravati River is the nearest water source, at a distance of 14.2 km, with southern tropical dry deciduous forests as the dominant vegetation.

Study Site III: Dechilpeta

The nesting site of WRV lies in the paddy fields of Dechilpeta village, Sironcha Forest Division, Maharashtra. The species constructed nests on taller palm trees (*Borassus flabellifer*) located at the middle of the field. The geo-coordinates of the location are 19°17.61" N, and 80°15'39.71" E, with the Indravati River being the nearest water body.

Breeding phenology

Data on breeding phenology were collected based on fortnightly surveys conducted for population studies at the breeding colonies of LBV at Palarapu Cliff during 2010–2021, Lakkameda Cliff during 2015–2021, and WRV in Dechilpeta during 2014–2021.

In the case of LBV, breeding starts with active soaring and gliding by the breeding pair in areas nearby the breeding cliff and ends with the first flight of chicks (Naoroji, 2006; Kanaujia et al., 2015). While in WRV, breeding begins with courtship flights consisting mainly of mutual circles in nearby breeding site and ends with successful fledgling of young (Collar et al., 2001; Naoroji, 2006; Kushwaha et al., 2009; Morinul and Khan, 2013). From the onset of breeding to the late chick-rearing period, each nest was monitored on a periodic basis, mostly on alternate days. Observations were made at a distance of 200 m from

the breeding colony and nests of territorial pairs were marked and monitored using Carl Zeiss 10×50 binoculars and a Nikon P900 camera. Mating birds identified repeatedly at the breeding colony during pre-laying season were considered as territorial pairs; those that laid eggs were defined as breeding pairs (Fernández et al., 1998; Xirouchakis, 2010). Dates of each phase, viz., nest-construction and copulation, egg-laying, incubation, hatching, and fledgling were noted by direct observation and were taken as the midpoint between two repeated visits when change in nest activity was noticed (Mendelson and Leshem, 1983; Leconte, 1985; Xirouchakis, 2010). Between 2010 and 2021, 78 focal nests of LBV were thoroughly monitored, which in total produced 51 eggs. Similarly, between 2014 and 2021, 67 focal nests of WRV were intensively monitored, which together produced 58 eggs. Details of the year-wise number of nests available, active nests, and focal nests for each nesting location are given in Supplementary Table.

Hatching success was defined as the proportion of eggs hatched per number laid, fledgling success as the proportion of chicks fledged per egg hatched, breeding success as the number of chicks fledged divided by the number of breeding pairs (clutches), and productivity as the number of chicks fledged divided by the number of territorial pairs (Cheylan, 1981; Xirouchakis, 2010). Nest success was the proportion of active nests that fledged at least one young. Nesting rate was determined by the percentage of territorial pairs that actually laid eggs. In addition, following parameters were considered to set a time for breeding failures.

Breeding pair observed in the nest, not start breeding

During the nest-construction period, copulation was observed but no eggs laid.

Breeding failure during incubation

Interval between the laying of the first egg to the last week of incubation, in LBV <55 days and in WRV <66 days.

Breeding failure during hatching

In LBV, 8–9 weeks and in WRV, 9–10 weeks.

Breeding failure during chick rearing

This period starts from nestling to before fledgling.

Data analysis

Statistical tests were performed using the SPSS software version 23. Breeding parameters are presented as mean ± standard error. A Kruskal–Wallis test was used to test the variation among the years in breeding phenology, while difference in breeding success and productivity among the years of study were tested using ANOVA. To know whether the proportion of fledgling success was similar to the proportion of hatching success G-tests for independence were used.

Results

Breeding phenology of Long-billed vulture

Nest construction and copulation

The mean date of nest construction and copulation of LBV was 28 October (range: 14 October–10 November), with a peak during late October and early November (Fig. 2A) and the same varied among years (Kruskal–Wallis: $H_{10} = 26.76$, $P = 0.003$).

Egg-laying dates and incubation

The mean egg laying date was 14 December (range: 05 December–21 December) with clutch size of single egg laid and the egg laying observed mostly during the latter half of December (92%) (Fig. 2B) without inter-annual variation (Kruskal–Wallis: $H_9 = 10.96$, $P = 0.28$).

Length of incubation period ranged from 53 to 55 days with a mean of 54 ± 1 days and with no inter-annual variation ($F_{9, 50} = 0.46$, $P = 0.89$). Both female and male incubated on brood, sex could not be differentiated due to the monogamous nature of co-habitation. Hatching observed from 01 to 12 February, with the first week of February being the peak (Fig. 2C) with no significant difference in hatching dates among the years (Kruskal–Wallis: $H_9 = 9.17$, $P = 0.42$).

Nestling and fledgling period

The nestling period was 103 ± 2 days with significant inter-annual variation ($F_{9, 36} = 4.35$, $P = 0.001$). Fledgling dates observed from 11 May to 01 June; more individuals fledged out during the third week of May and less during the first week of June (Fig. 2D) with insignificant variation in fledgling dates among the years (Kruskal–Wallis: $H_9 = 10.72$, $P = 0.3$).

Breeding phenology of White-rumped vulture

Nest construction and copulation

The mean nest construction and copulation date was 07 October (range: 02–12 October); the same was displayed in October (Fig. 3A) with significant inter-annual variation (Kruskal–Wallis: $H_5 = 14.84$, $P = 0.011$).

Laying dates and incubation

The mean laying date was 14 October (range: 07–20 October) with a single clutch size, and the eggs mostly laid during the second week of October (Fig. 3B) with significant variation among the years (Kruskal–Wallis: $H_5 = 19.31$, $P = 0.002$).

The length of the incubation period ranged from 57 to 66 days with a mean of 61 ± 1 days with significant inter-annual variation ($F_{5, 57} = 11.55$, $P = 0.000$). Both males and females incubated the eggs. Hatching was observed from 02–21 December, peaking during the third week of December (Fig. 3C),

with significant inter-annual variation (Kruskal–Wallis: $H_5 = 34.64$, $P = 0.000$).

Nestling period and fledgling period

The nestling period for chick rearing was 105 ± 1 days with significant inter-annual variation ($F_{5, 52} = 5.99$, $P = 0.000$). The fledgling dates ranged from 19 March to 05 April, with more fledglings observed during the fourth week of March (Fig. 3D) and no significant variation in fledgling dates among years (Kruskal–Wallis: $H_5 = 6.75$, $P = 0.24$). After the first flight, the nestling was considered as fledgling, prior to which nestlings flapped their wings in the nest and jumped on branches.

Breeding parameters

A total of 159 territorial pairs of LBVs were identified in 12 years from two sites, of which 115 laid eggs and 85 raised the chicks successfully (Table 1). The proportion of eggs hatching per number of egg laying (hatching success) and the proportion of successful fledgling per egg hatching (fledgling success) were similar (78.05% vs. 70.87%, $G = 0.56$, $df = 18$, $P > 0.1$).

The breeding success and productivity of LBV were, respectively, 0.72 ± 0.08 and 0.52 ± 0.07 , and no significant inter-annual variation was recorded in breeding success and productivity (Table 1), (breeding success: $F_{11, 18} = 0.46$, $P = 0.88$; productivity: $F_{11, 18} = 1.6$, $P = 0.3$). The percentage of nesting rate of LBV was 64 ± 7.1 . The overall nest success of LBV was 78 ± 4.4 (range: 33%–100%) and out of 23 nests, 7 showed 100% success.

A total of 124 territorial pairs of WRV were identified over six years, of which 114 laid eggs and 104 raised chicks successfully (Table 2). The proportion of eggs hatching per number of egg laying (hatching success) and the proportion of successful fledgling per egg hatching (fledgling success) were similarly high (97.0% vs. 87.9%, $G = 0.18$, $df = 8$, $P = 0.65$).

The breeding success and productivity of WRV were, respectively, 0.85 ± 0.1 and 0.83 ± 0.1 , and no significant variation was seen in breeding success and productivity over the years (Table 2) ($F_{5, 8} = 0.15$, $P = 0.97$; $F_{5, 8} = 0.13$, $P = 0.98$). The mean percentage of nesting rate of WRV was 85 ± 10.8 . The nest success of WRV was 91.9 ± 2.5 (range: 50%–100%), and 27 out of 38 nests showed 100% nest success.

Timing of breeding failure

In total, out of 159 breeding attempts observed over the 12-year period (2010–2021), for LBV, no egg was laid in 44 cases (28%), though courtship display, copulation, and nest building were observed in each case. Of the 15 nests (2010–2014) at Palarapu Cliff and 8 (2015–2021) at Lakkameda Cliff, a total of 23, fluctuation in egg laying was observed among the years. Thirty (19%) breeding attempts failed and eighty-five (53%) succeeded.

Among the 30 breeding failures, 6 (20%) were during incubation, 8 (26.7%) during hatching, and 16 (53.3%) during chick rearing (Table 3).

Of the total 124 breeding attempts monitored over the period of six years (2014–2021) for WRV, no egg was laid in 10 cases (8%), even though courtship display, copulation, and nest building were observed. Egg

laying was observed in 8 nests (2014–2015) near Dechilpeta, and in 25–30 nests (2018–2021) at Dechilpeta. A total of 10 (8%) breeding attempts failed and 104 (84%) succeeded. Among the 10 breeding failures, 3 (30%) failed during incubation, 4 (40%) during hatching, and 3 (30%) during chick rearing. The highest failure occurred during egg laying and hatching (Table 4).



Figure 1: (A) Panoramic view of breeding colony of LBV, Palarapu Cliff; (B) Pair of LBV in Peddavagu stream; (C) LBV at the nest with egg; and (D) LBV with nestling.

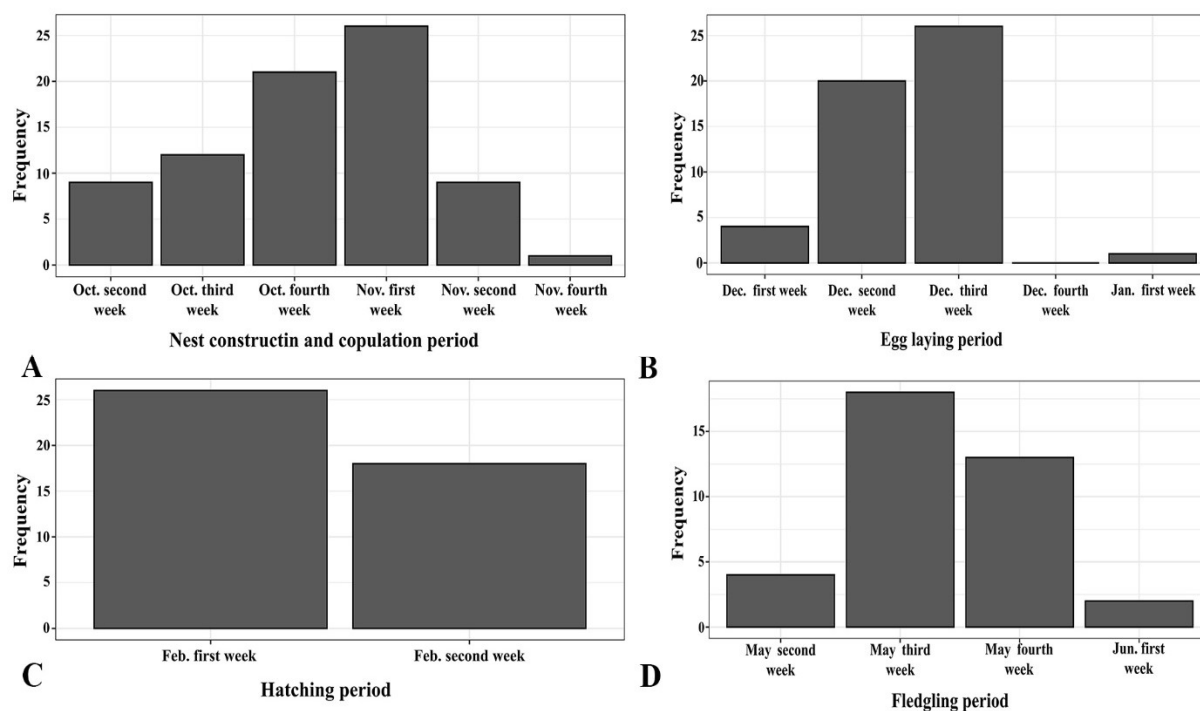


Figure 2: Breeding phenology of Long-billed vulture observed at Palarapu cliff and Lakkamedda cliff during 2010–2021. Nest construction and copulation period (A), egg laying period (B), hatching period (C), and fledging period (D).

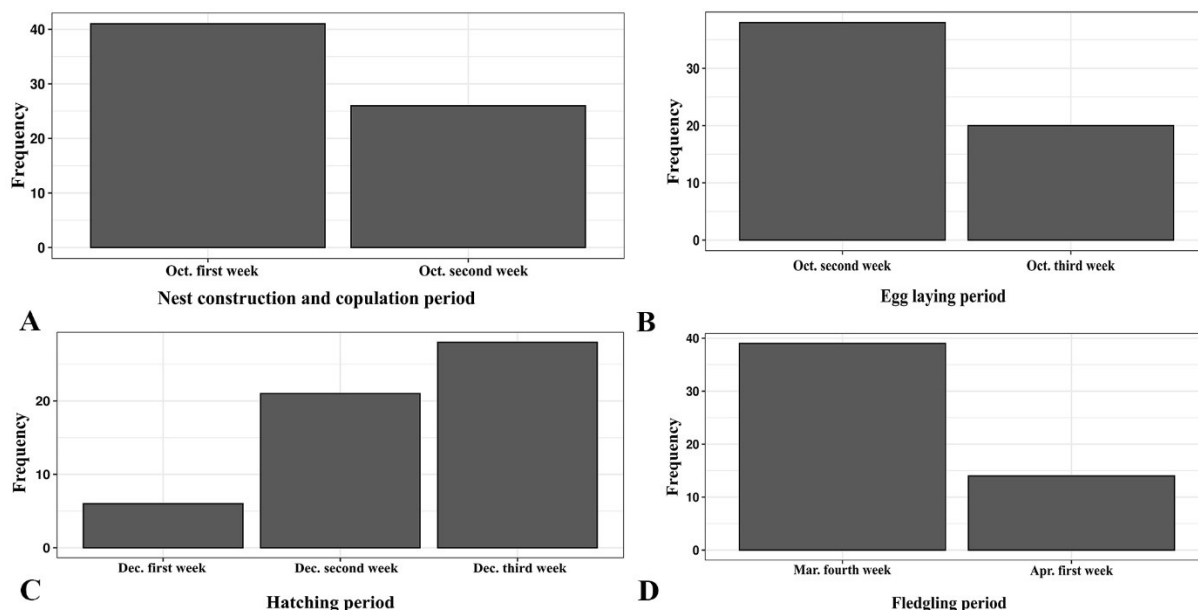


Figure 3: Breeding phenology of White-rumped vulture observed at Dechilpeta during 2015–2021. Nest construction and copulation period (A), egg laying period (B), hatching period (C), and fledgling period (D).

Table 1: Reproductive performance of critically endangered Long-billed vulture (*Gyps indicus*) in Kaghaznagar and Sironcha Forest Divisions during 2010–2021.

Location	Year	Territorial pairs	Breeding Pairs (Clutches)	Successful pairs (Fledglings)	Nesting rate (%)	Breeding success	Productivity
Palarapu Cliff (Site I)	2010	8	7	6	87.5	0.86	0.75
	2011	7	3	3	42.9	1.00	0.43
	2012	10	7	6	70.0	0.86	0.60
	2013	9	8	8	88.9	1.00	0.89
	2014	10	8	7	80.0	0.88	0.70
	2015	10	8	7	80.0	0.88	0.70
	2016	11	10	6	90.9	0.60	0.55
	2017	12	9	7	75.0	0.78	0.58
	2018	12	8	7	66.7	0.88	0.58
	2019	15	11	1	73.3	0.09	0.07
	2020	8	5	0	0.0	0.00	0.00
2021	0	0	0	0.0	0.00	0.00	
mean ± SE for Site I		9 ± 1	7 ± 1	5 ± 1	62.9 ± 9.2	0.65 ± 0.1	0.49 ± 0.09
Lakkameda Cliff (Site II)	2015	5	5	4	100.0	0.80	0.80
	2016	7	6	6	85.7	1.00	0.86
	2017	8	7	7	87.5	1.00	0.88
	2018	8	3	2	37.5	0.67	0.25
	2019	8	3	2	37.5	0.67	0.25
	2020	7	6	5	85.7	0.83	0.71
	2021	4	1	1	25.0	1.00	0.25
mean ± SE for II site		7 ± 1	4 ± 1	4 ± 1	65.6 ± 11.6	0.85 ± 0.06	0.57 ± 0.12
Irrespective of site mean ± SE (n)		8 ± 1 (159)	6 ± 1 (115)	4 ± 1 (85)	64 ± 7.1	0.72 ± 0.08	0.52 ± 0.07

Table 2: Reproductive performance of critically endangered White-rumped vulture (*Gyps bengalensis*) in Sironcha Forest Division during 2015–2021.

Year	Colony	Territorial pairs	Breeding pairs (Clutches)	Successful pairs (Fledglings)	Nesting rate (%)	Breeding success	Productivity
2014	Chelwada	1	1	1	100.0	1.00	1.00
2014	Damrancha	2	1	0	0.0	0.00	0.00
2014	Khandla	5	5	5	100.0	1.00	1.00
2015	Chelwada	1	1	1	100.0	1.00	1.00
2015	Khandla	5	5	5	100.0	1.00	1.00
2018	Dechilpeta	25	22	20	88.0	0.91	0.80
2019	Dechilpeta	25	23	22	92.0	0.96	0.88
2020	Dechilpeta	30	28	25	93.3	0.89	0.83
2021	Dechilpeta	30	28	25	93.3	0.89	0.83
Mean ± SE (n)		14 ± 4 (124)	13 ± 4 (114)	12 ± 4 (104)	85 ± 10.8	0.85 ± 0.1	0.82 ± 0.1

Table 3: Timing of breeding failure of Long-billed vulture in Kaghaznagar and Sironcha Forest Divisions during 2010–2021.

Year	2010	2011	2012	2013	2014	2015	2016	2017	2018	2019	2020	2021
Pairs did not start breeding	1	4	3	1	2	2	2	4	9	9	4	3
Breeding failure during incubation	0	0	0	0	0	1	0	0	1	3	1	0
Breeding failure during hatching	0	0	0	0	0	1	0	0	1	3	3	0
Breeding failure during chick rearing	1	0	1	0	1	1	4	2	1	4	1	0

Table 4: Timing of breeding failure of White-rumped vulture in Sironcha Forest Division during 2015–2021.

Year	2014	2015	2018	2019	2020	2021
Pairs did not start breeding	1	0	3	2	2	2
Breeding failure during incubation	0	0	0	0	1	2
Breeding failure during hatching	0	0	1	1	1	1
Breeding failure during chick rearing	1	0	1	0	1	0

Discussion

This study is the first long-term assessment of the breeding ecology of LBV and WRV in India that evaluated both breeding phenology and reproductive performance through continuous monitoring in three different nesting colonies between 2010 and 2021. This study, with its empirical data, demonstrates that the breeding success and productivity of LBV and WRV are declining significantly over the years.

LBV breeding phenology

The timing of the breeding and nesting season of LBV, observed in this study from October to May, is consistent with earlier studies (Naoroji, 2006; Chetan et al., 2017). In the present study, nest construction was observed from mid-October to late November with a peak during the last week of October and the first week of November. The copulation frequency was also observed to increase with the nesting peak. It is likely that nest construction at the offset of monsoon enables the breeding pairs to gather nest materials like tall grass easily, as plants attain maximum growth after rains. Further, nest construction at the end of monsoon is advantageous as ledges are not affected by rains. In addition, it could also be a factor associated with the reproductive physiology of the species concerned and carcass availability or mortality pattern of large herbivores that act as the major food source of these vultures.

Female LBV laid a single egg during December, with slight variation in time at the end of November at Chambal River, Rajasthan. Nevertheless, egg laying varied in other regions that began as early as November in Baroda and as late as 03 March in Nilgiris (Baker, 1935). The incubation period ranged from 53 to 55 days with a mean of 54 ± 1 days, which

is similar to the minimum of 50 days reported by Naoroji (2006) but different from that reported by Chetan et al. (2017) (62.5 ± 1.5 days). Hatching was observed from 01–12 February, with the first week of February being the peak in this study. The hatching peak was previously reported as early as 22 January in Chambal River (Chetan et al., 2017). The nestling period observed was 103 ± 2 days, which varied from that in Chambal River (129.4 ± 1 days); after the first flight, the nestling period is considered as fledgling, prior to which, nestlings flapped their wings in the nest and jumped on the ledge and other places on the cliff with fledgling observed from 11 May to 01 June, but more individuals fledged out in the third week of May. The peak fledgling date in Chambal River was previously reported on 05 April (Chetan et al., 2017).

WRV breeding phenology

Breeding season varies locally and extends from September to June (Jones, 1916 in Naoroji, 2006), but the present study showed that WRV breed from October to April, similar to that reported by Baral et al., (2005) and Khan (2013) from other locations. Unlike LBV, no other study with long-term data is available on WRV for the comparison of breeding biology and reproductive performance results. Based on the present study, nest construction started in October and all nests were built on *Borassus flabellifer*.

Nesting after monsoon may be advantageous for having a clean nest, as excreta and previously used nesting material get washed out by heavy rains. The mean date of nest construction was 07 October (range: 02–12 October), with the peak period in the first week of October; copulation was also taking place at the time of nesting. Female WRV laid a single egg during the second and third weeks of October.

Both parents incubated the egg, with the incubation period at 57–66 days, which is comparable with 50–60 days reported by Samson and Ramakrishnan (2020), but higher than the minimum of 45 days reported by Ali and Ripley (1978). Our finding is similar to that reported for the White-backed vulture *Gyps africanus* (Salvadori, 1865) of 56 days (Naoraji, 2006). Hatching was observed during 02–21 December, with the peak during the third week of December, which is one month in advance of that reported in the second week of January in Sigur Plateau, Tamil Nadu by Samson and Ramakrishnan (2020). There were no previous observations on the nestling period; our results showed it as 105 ± 1 days and fledgling dates ranged from 19 March to 05 April, with more fledglings observed during the fourth week of March.

Reproductive performance

The present study showed that breeding success and productivity varied spatiotemporally in the case of LBV and temporally in WRV. Spatially, the breeding colony size is related to the breeding success of the group of living birds (Hunt et al., 1986; Barbosa et al., 1997; Brunton, 1997; Weaver and Brown, 2005). The optimum group size depends on the definition of fitness (Sibly, 1983; Kramer, 1985; Giraldeau and Gillis, 1985) and colonies of intermediate size had relatively better breeding success than large or smaller colonies as reported in Griffon vultures (Leconte, 1985; Arroyo et al., 1990; Xirouchakis, 2010). Our study was limited to a maximum of two breeding colonies in the case of LBV, unlike studies on Griffon vultures that had multiple breeding colonies (Leconte, 1985; Arroyo et al., 1990). The larger breeding colony of LBV at Palarapu Cliff with more active nests ($n = 84$) experienced a lower rate of breeding success (65%) than the one at Lakkamedda Cliff that had a smaller number of active nests ($n = 31$) with a higher rate of (85%) breeding success. However, there exists a contradicting trend in LBV, i.e., higher breeding success with both smaller number of active nests (100% breeding success out of two active nests reported by Chandni et al. (2018)) and a larger number of active nests (90% breeding success out of 92 active nests reported by Chhangani (2004)). Additionally, in the present study temporal variation in the breeding success of LBV was observed from 0% (in 2020 and 2021) to 100% (in 2011 and 2013) at Palarapu Cliff, and similarly in the case of WRV. A similar temporal variation in breeding success was also reported for LBV and WRV elsewhere in India (Munir et al., 2004; Chishty and Choudhary, 2020) and abroad (Bangladesh: Khan, 2013; Pakistan: Gilbert et al., 2002).

From the above discussion, it is clear that the reproductive performance varied spatiotemporally. Though breeding success is attributed to breeding colony size with a moderate colony size showing a higher success rate than a larger or smaller colony size, the contradicting results indicate that apart from the size of the breeding colony, other factors like climate,

nest, nest-site characteristics, and carcass availability could contribute to the spatiotemporal variation in their breeding success. Therefore, future studies need to consider assessing the ecological factors driving breeding performance, so that specific measures can be taken to positively influence the breeding and population size to ensure the long-term conservation of these threatened species.

Further, this study showed a drastic decline in the breeding success of LBV at Palarapu Cliff since 2019. Although the present study did not evaluate the actual cause for the decline, poisoning of cattle carcasses reported by local people in 2018 in and around the study area, could be a significant contributor. Similarly, in 2017, the Sirpur Paper Mills, one of the largest manufacturers of color paper, reopened in Kaghaznagar, Asifabad District, and it discharges its hazardous effluent into the Peddavagu stream. This stream is the local lifeline for humans, cattle, and wild animals, including the critically endangered LBV at Palarapu Cliff. It merges with River Pranahita near Palarapu Cliff. The effluent-polluted water resulted in the death of a large number of cattle and LBV in 2005, which evoked a large public protest against the paper industry. Since its reopening, vulture mortality was observed more frequently, increasing the suspicion of the continued threat of poisoning with toxic substances in the environment. Poisoning due to agricultural pesticides and baits used to kill large carnivores, also kill vultures incidentally (Clement et al., 2013; Ogada et al., 2016; Hernández and Margalida, 2018). The feeding ecology and sociality of vultures make them vulnerable to various risks, including environmental changes, poisoning, and bioaccumulation of toxic substances from agricultural pesticides and veterinary drugs used in cattle (Di Vittorio et al., 2018). Poisoning is the most important threat, affecting 78% of vultures across globe (Plaza et al., 2019). In recent years, the news media often warns that poisoning of carcasses causes more vulture deaths in Assam, north-east India. Therefore, in light of the present study, the following measures are suggested: (i) Long-term monitoring of breeding colonies with more detailed ecological aspects, including drivers of population size and structure, breeding conditions, telemetry-based range assessment, and molecular and toxicological studies. (ii) Implementation by all state forest departments of Vulture Safe Zones proposed by the Ministry of Environment, Forest and Climate Change, Government of India in 2014. (iii) Application of threat analysis approaches in future studies for ranking the threats in decreasing order using an expert-based approach as outlined by earlier studies so as to improving the practice of conservation (Salafsky et al., 2002, 2008). These efforts would not only provide a better understanding of the ecology of critically endangered *Gyps* vultures but would also save them from local extinction.

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Author contributions

R.M. carried out field survey, taken care of methodology, data collection, preliminary compilation of data and the first draft of manuscript. N.B. conceived the concept, data curation, formal analysis, supervision, validation, visualization, final draft and review and editing of manuscript.

Conflict of interest

The authors declare that there is no conflicting issue related to this research article.

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Supplementary Table: Details of number of nests of Long-billed and White-rumped vultures under observation, and the number of egg-laid, hatched and fledged during study period in different nesting colonies in Kaghaznagar and Sironcha Forest Divisions.

Species	Nesting Place	Year of study	Active Nest	Focal Nest	No. of eggs laid	No. of chicks	No. of fledglings
LBV	Palarapu Cliff	2010	7	5	7	7	6
LBV	Palarapu Cliff	2011	4	4	3	3	3
LBV	Palarapu Cliff	2012	7	5	7	7	6
LBV	Palarapu Cliff	2013	9	6	8	8	8
LBV	Palarapu Cliff	2014	9	7	8	8	7
LBV	Palarapu Cliff	2015	8	5	8	8	7
LBV	Palarapu Cliff	2016	10	6	10	10	6
LBV	Palarapu Cliff	2017	9	6	9	9	7
LBV	Palarapu Cliff	2018	8	5	8	8	7
LBV	Palarapu Cliff	2019	11	9	11	4	1
LBV	Palarapu Cliff	2020	5	2	5	0	0
LBV	Palarapu Cliff	2021	0	0	0	0	0
LBV	Lakkamedda Cliff	2015	5	3	5	4	4
LBV	Lakkamedda Cliff	2016	6	4	6	6	6
LBV	Lakkamedda Cliff	2017	7	3	7	7	7
LBV	Lakkamedda Cliff	2018	7	3	3	2	2
LBV	Lakkamedda Cliff	2019	5	2	3	3	2
LBV	Lakkamedda Cliff	2020	6	3	6	6	5
LBV	Lakkamedda Cliff	2021	3	0	1	1	1
LBV	Overall		126	78	115	101	85
WRV	Chelwada	2014	1	1	1	1	1
WRV	Damrancha	2014	1	2	1	1	0
WRV	Khandla	2014	5	5	5	5	5
WRV	Chelwada	2015	1	1	1	1	1
WRV	Khandla	2015	5	1	5	5	5
WRV	Dechilpeta	2018	24	14	22	21	20
WRV	Dechilpeta	2019	24	12	23	22	22
WRV	Dechilpeta	2020	29	13	28	26	25
WRV	Dechilpeta	2021	28	18	28	25	25
WRV	Overall		118	67	114	107	104