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NESTING SUCCESS AND NEST-SITE SELECTION OF WHITE-RUMPED VULTURES (*GYPES BENGALENSIS*) IN WESTERN MAHARASHTRA, INDIA

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ABSTRACT.—A few breeding populations of White-rumped Vultures (*Gyps bengalensis*) still survive in pockets of their original vast range in India, having weathered a diclofenac-induced population decline of 99.9% since the early 1990s. These breeding populations are potential sources of recruits, now that the overall population appears to be stabilizing or even recovering in some areas. We studied two White-rumped Vulture nesting colonies in the Raigad district of coastal Maharashtra in 2013–2014, to investigate site-specific nesting success and nest-site selection. Our overall aim was to better understand the capability of these remnant populations to contribute to the stability of vulture populations at a landscape scale. We found that vultures preferred to nest in taller trees. Nest failure was high before hatching but declined thereafter. Overall nesting outcome was unrelated to the distance of the nest from areas of disturbance, but may have been influenced by characteristics of nest trees. The percentage of successful nests was higher in the smaller colony, suggesting that colony size may not be the only best criterion for targeting conservation efforts.

KEY WORDS: *White-rumped Vulture*, *Gyps bengalensis*; *breeding*, *critically endangered*; *Gyps*; *India*; *nest*; *nesting success*.

ÉXITO DE CRÍA Y SELECCIÓN DEL SITIO DE NIDIFICACIÓN DE *GYPES BENGALENSIS* EN MAHARASHTRA OCCIDENTAL, INDIA

RESUMEN.—Unas pocas poblaciones reproductivas de *Gyps bengalensis* sobreviven aún en reductos de su amplia área de distribución original en India, tras haber sufrido una disminución del 99.9% de la población inducida por diclofenaco desde principios de la década de los 90. Estas poblaciones reproductivas son fuentes potenciales de reclutas, ahora que la población en general parece estar estabilizándose o incluso recuperándose en algunas áreas. Estudiamos dos colonias de cría de *G. bengalensis* en el distrito de Raigad en la costa de Maharashtra en 2013–2014, para investigar el éxito de cría específico del sitio y la selección del sitio de nidificación. Nuestro objetivo general fue comprender mejor la capacidad de estas poblaciones remanentes para contribuir a la estabilidad de las poblaciones de buitres a escala de paisaje. Encontramos que los buitres preferían anidar en los árboles más altos. El fracaso de nidos fue alto antes de la eclosión, pero disminuyó a partir de entonces. El resultado general de la cría no estuvo relacionado con la distancia del nido a las áreas de molestias, pero puede haber estado influido por las características de los árboles con nidos. El porcentaje de nidos exitosos fue mayor en la colonia más pequeña, lo que sugiere que el tamaño de la colonia puede no ser el único criterio clave para focalizar los esfuerzos de conservación.

[Traducción del equipo editorial]

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The dramatic decline of *Gyps* vulture populations has drawn global attention to their conservation in the past two decades. The Indian subcontinent has seen particularly large changes, with populations beginning to collapse in the early 1990s (Cunningham et al. 2003). Prior to this, *Gyps* vultures occurred at remarkably high densities and were abundant across most of India (Wilbur and Jackson 1983, Prakash et al. 2003). They were major scavengers, reaching particularly high densities in human-dominated landscapes, where their primary source of food was carrion from domestic ungulate carcasses (Pain et al. 2003). The decline of three *Gyps* species, White-rumped Vulture (henceforth, WRV; *G. bengalensis*), Long-billed Vulture (*G. indicus*), and Slender-billed Vulture (*G. tenuirostris*), along with other vultures such as the Egyptian Vulture (*Neophron percnopterus*) and the Red-headed Vulture (*Sarcogyps calvus*; Galligan et al. 2014), across the Indian subcontinent was attributed largely to the consumption of tissue from carcasses of individual cattle that had recently been administered with the nonsteroidal anti-inflammatory drug diclofenac (Shultz et al. 2004). This drug causes visceral gout, kidney failure, and death in *Gyps* vultures (Swan et al. 2006). High mortalities due to secondary poisoning, exacerbated by the naturally slow breeding rate of vultures (Sarrazin et al. 1994), necessitated immediate conservation actions. These included a ban on the use and manufacture of veterinary diclofenac as well as the establishment of breeding centers for *Gyps* vultures to maintain viable populations (Bowden et al. 2012). Although there is evidence of continued poisoning (Cuthbert et al. 2015), recent surveys suggest that population declines have slowed (Cuthbert et al. 2011, Prakash et al. 2012, 2017) and it is likely that remnant wild populations that escaped major diclofenac poisoning will play a key role in population recovery.

Because remnant populations are poorly understood, studying and monitoring their breeding performance can help researchers identify recruitment bottlenecks and key drivers of breeding success. Such information has proved useful for conservation management (Donazar et al. 1993) in other species like the Egyptian Vulture (*Neophron percnopterus*) on the Italian peninsula (Liberatori and Penteriani 2001) and the Cinereous Vulture (*Aegypius monachus*) in Iberia (Morán-López et al. 2006).

Nesting success of *Gyps* vultures has been monitored for one or more breeding seasons at colonies in parts of the geographical range of WRVs, such as

Nepal, Pakistan, Bangladesh, and parts of northern and western India. Declining nesting success in Nepal (Baral and Gautam 2007) and Bangladesh (Monirul and Khan 2013) was likely due to diclofenac poisoning; in contrast, nest success of WRV increased in Maharashtra, India, between 2004 and 2011 (Pande et al. 2013).

Such site-based studies that generate information about nesting success and requirements of existing colonies are needed to identify and form effective “Vulture Safe Zones” (Bowden et al. 2012). They could also prove of vital importance for potential reintroduction of captive-bred vultures to these areas, because reintroduced individuals are likely to nest around or with existing colonies (Prakash et al. 2003). Conservation strategies, such as the protection of specifically chosen nesting trees, can also be proposed following such investigations, as there is evidence of choice of specific trees in other areas (Baral and Gautam 2007, Thakur and Narang 2012).

We studied two nesting colonies of WRV located in different habitats in the Raigad district of Maharashtra, India, to estimate overall breeding performance and to investigate nest-site selection. The specific objectives of this study were to (1) compare nesting success between the two colonies, (2) examine nest-site selection of breeding pairs at both sites, and (3) assess whether nest-site choice at the scale of individual nesting trees is associated with nesting outcome. Nesting success may act as an indicator of the habitat suitability at these sites, and specific small-scale habitat measurements may help reveal which habitat features vultures select and how those choices may influence reproductive success. The results of our investigations should inform a site-specific understanding of the nesting ecology of a species of high conservation concern and allow managers to develop strategies that promote enhanced nesting success.

METHODS

Study Site. This study was conducted in the coastal district of Raigad in the state of Maharashtra, at two WRV nesting colonies located in two subdistricts, Shrivardhan and Mhasla (Fig. 1). These nesting colonies have been a part of annual monitoring surveys by two conservation organizations, Sahyadri Nisarga Mitra and the Society of Eco-Endangered Species Conservation and Protection, since at least 2004.

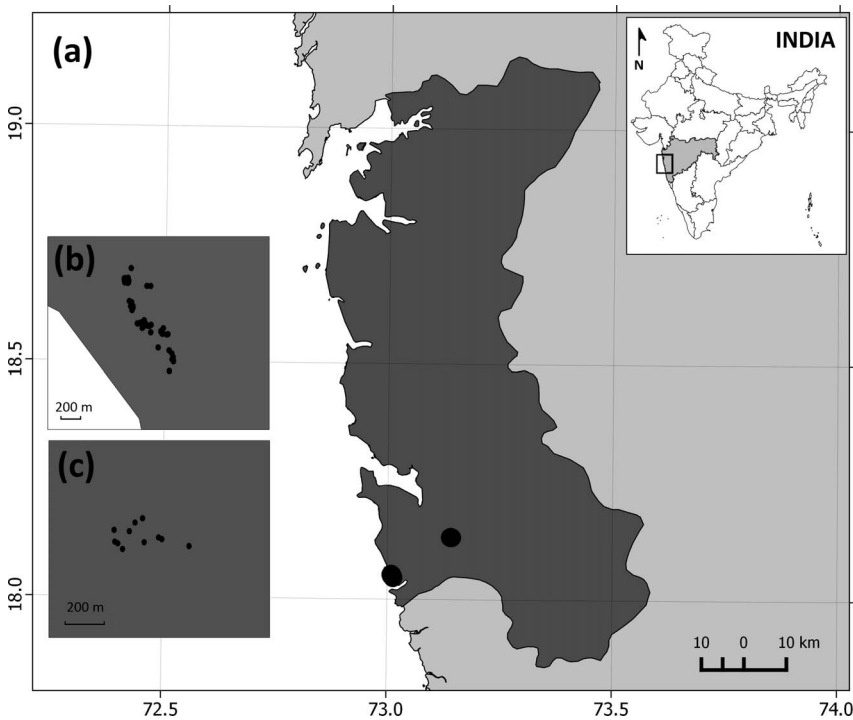


Figure 1. (a) Locations of two nesting colonies of White-rumped Vultures in Raigad district, Maharashtra, India; (b) distribution of nests in the Shrivardhan plantation colony; and (c) distribution of nests in the Mhasla forest colony.

The Shrivardhan colony (hereafter, “plantation colony”) was located in the coastal town of Shrivardhan ($18^{\circ}2.88'N$, $73^{\circ}1.14'E$), and covered approximately 0.5 km^2 . The habitat consists largely of contiguous stretches of coconut (*Cocos nucifera*) and areca nut (*Areca catechu*) plantations interspersed with houses and agricultural plots. At least 25 nests were present in this colony in each of the previous four years (Sahyadri Nisarga Mitra unpubl. data).

The Mhasla colony (hereafter, “forest colony”) is adjacent to a village of approximately 30 households, ca. 16.5 km northeast ($18^{\circ}7.92'N$, $73^{\circ}8.46'E$) of the plantation colony. The extent of the colony was approximately 0.10 km^2 in mixed deciduous forest, with dominant tree species including *Mangifera*, *Terminalia*, *Erythrina*, *Bombax*, and *Ficus*. Nesting has been monitored here since 2004 and nest counts have increased from 2 to 16 between 2004 and 2011 (Pande et al. 2013).

Nest Searches and Apparent Nesting Success. WRVs generally begin breeding in October (Gilbert et al. 2007), and we started nest searches on foot at both colonies in early November 2013, when early nests were expected to be in the incubation stage.

Searches continued throughout the breeding season, so that we could identify any late nests. Although WRVs typically lay only a single egg (Ali and Ripley 1968), if they initiate multiple broods within one breeding season, there may be more nests than breeding pairs reported from a colony. Partially built nests were not included in our analysis.

We monitored nests approximately every 15 d using binoculars or a spotting scope from at least 5 m from the nest tree. To minimize disturbance, we did not attempt to directly determine nest contents (e.g., through climbing or using a mirror/camera on a pole). Observation sessions started on 23 November 2013 in the plantation colony and on 2 December in the forest colony. The first two observation sessions at each nest at the former and the first session at the latter were 15 min long; subsequent sessions were increased to 120 min.

Based on the time adults were present at the nest, nests were categorized as either occupied (i.e., at least one adult was in attendance at the nest for >1 min) or unoccupied (if no adult was in attendance for two consecutive sampling occasions). We inferred incubation or brooding if an adult was sitting

tightly on the nest for >1 min of an observation session. Observation sessions were terminated after a nestling was seen and subsequent observation sessions lasted only long enough to confirm the continued presence (or absence) of the nestling. When we found a nest destroyed, or documented egg or nestling mortality, we classified the nest as unsuccessful. We classified a nest as successful when we observed the young perched outside the nest or exercising its wings (occurs a few days prior to fledging).

We divided nesting into four stages: initiation, mid-incubation, nestling stage, and fledging, and each occupied nest was assigned one of these stages at each observation session, using the following criteria. For those nests where the young were visible during observations, we estimated the nestling age based on photographs from *Gyps* breeding centers and back-calculated to determine hatching and laying dates. For this, we assumed an incubation period of 55 d (range 50–60 d for WRV; Gilbert et al. 2002). For nests that failed before a nestling could be seen, we had only a record of the number of days such a nest was occupied by adults; based on this number, we made a conservative estimate of the nesting stage, to allow us to calculate an overall apparent nesting success. We here use the term “apparent” to indicate that only known nests from the colony were considered (Jehle et al. 2004). Because WRV nests are conspicuous and this species displays nesting synchrony in their colonies, we assumed minimal bias from a lack of detection of failed nests (Mayfield 1961, Johnson and Shaffer 1990).

Based on the above, every occupied nest was assigned a stage as of the end of November or early December (when sampling commenced at both colonies) and the counts of nests were compared by nest stage between the two colonies. Nests found during construction were grouped separately because estimating the nesting stage based on occupied days was not required. We determined the number of nests that survived to each nesting stage. For nests that failed, we assumed the failure date was halfway between the last visit at which the nest was occupied and the subsequent visit. We estimated (1) stage-wise nest success and (2) overall nest success by calculating (1) the proportion of nests that reached the succeeding stage from the previous one and (2) the proportion of all occupied nests that fledged a young.

Nest-Site Selection. To examine nest-site selection by WRVs, we matched each nest tree with nearby unused (available) trees (Bonnot et al. 2009, Lele et al. 2013). We chose three of these unused nearby trees in a matched design, such that each was from a different random quadrant (NE, NW, SE, or SW; no quadrant repeated), and at a randomly chosen distance between 20 and 30 m from the nest tree. This procedure produced 144 and 33 matched unused trees for the plantation and forest colonies, respectively. Because nests were found only in coconut trees in the plantation colony, we selected only coconut trees for the random, matched trees. In the forest colony, we sampled only unused trees that could reasonably support a WRV nest. In a small number of cases, when two nest trees were very close, one or more of their matched unused trees were common to both.

A few trees contained more than one nest, and therefore the number of nest trees (48 and 11 in the plantation and forest colonies, respectively) was fewer than the number of nests (49 and 17, respectively). We included each nest tree, even those containing multiple nests, only once in our data set. We measured several variables at each nest tree and the area immediately surrounding it (Table 1) at both sites, except that canopy leaf count was only relevant (and therefore only measured) at the plantation colony.

Analyses. We examined nest-site selection separately at each of the sites. Differences between used and unused trees were visualized using line plots and supplemented by calculations of the average used–unused difference for each variable, with 95% bootstrapped confidence intervals around the mean difference. We also performed logistic regression to substantiate our findings from the above on the correlates of nest-site selection (see supplemental materials). However, the logistic regression was only performed on the plantation colony data due to sample-size constraints at the forest colony.

Correlates of Apparent Nest Success. For the plantation colony, we used a generalized linear model with binomial error structure to examine which predictors best explain nest success or failure. In addition to the potential predictors listed in Table 1, we also measured distances to the nearest open edge of the plantation, to nearest neighboring nests and inhabited houses, and to roads and construction sites (for the plantation colony only). If two potential predictors were correlated (i.e., $r > 0.70$), then we used only one of them. All predictors were stan-

Table 1. Nest-site variables measured at White-rumped Vulture colonies in western Maharashtra, India.

NEST-SITE VARIABLE	MEASUREMENT AND DESCRIPTION
Tree height (m)	Measured with handheld rangefinder
Girth at breast height (GBH; cm)	Measured with measuring tape
Lower canopy leaf count ^a	Counted the leaves in the lower canopy on a photo of the tree canopy from beneath.
Percent exposure ^b	Visually estimated in all four quadrants in a 30-m radius; (defined as the approximate area in a quadrant that is devoid of vegetation below a height of 2 m)
Tree count at 10 m ^c	Counted trees >2 m tall in circular plots of 5-m radius at 10 m and 20 m NE, SE, SW, and NW of the sampled tree.
Proportion of tall trees in a 10-m radius ^d	Divided the number of trees taller than the sampled tree by the total number of measured trees in the surrounding plot; (measured trees at 3, 6, and 9 m in eight directions around the sampled tree)

^a Provides an index of the area available for nest placement; measured only at plantation colony in coconut palms.

^b An estimate of ground-level openness.

^c An index to tree density in the area surrounding the tree.

^d Relative height.

standardized using Z-score conversions. We constructed a global model with all predictors (because “distance to edge” and “percent exposure” were highly correlated [$r = -0.79$], they were not considered in the global model together) and compared it to a null model and to competing models with single predictors and combinations of predictors. All models were additive and no interaction terms were considered. We first simplified the global model by dropping those predictors (in our case, six predictors) that had a high standard error associated with the predicted estimate and determined whether these simplified models ranked higher. We then performed model selection by constructing 16 competing models (with single predictors and various combinations), which we compared using Akaike Information Criterion (AIC; Burnham and Anderson 2002). Relative importance of predictors was assessed based on the model-averaged values of the predicted coefficient estimates and the associated standard errors. To examine fit, we compared observed and predicted values for each nest and calculated the proportion of nests correctly classified by the top models (within $\Delta\text{AIC} < 2.0$).

For the forest colony, due to low sample size ($n = 17$), we compared the measurements at successful and unsuccessful nests in univariate tests using bootstrapped means and nonparametric 95% confidence intervals.

We created a study area map using QGIS 2.16 (QGIS Development Team 2016). We performed all analyses using R 3.0.1, which we also used to generate the illustrations (R Core Team 2016). All

data are available for download at Data Dryad (doi:10.5061/dryad.11ng449).

RESULTS

We found 49 and 17 nests at the plantation and the forest colony, respectively. At the former, we found 36 nests in late November 2013, at the start of the study (i.e., “early nests”) and an additional 13 later in the season before February (i.e., “late nests”). Of the 13 late nests, 12 were found during the nest-building stage, and one was found after construction. Among these 12 nests, two were left unused and we never saw adults at them during our observation sessions; hence, these were not included in the occupied nest totals. In three instances among the late nests, we observed vultures transferring material from previously failed nests to the newly built ones.

Of the 17 occupied nests in the forest colony, nine were discovered at the start of the study in early December 2013 (the “early nests”), while eight were discovered later (termed “early nests that were discovered later”) in neighboring locations that had not been surveyed earlier in the nesting season. Seven of these eight contained a nestling when found. We found no nests that were built after early December.

Stage-Specific Apparent Nest Success. We assumed that all nests found at the start of the study had reached the mid-incubation stage, because more than half of these nests (17/24 at the plantation colony and 4/7 at the forest colony) were found at this stage.

In the plantation colony, 22% of early nests ($n = 36$) were successful, compared to 33% of the early

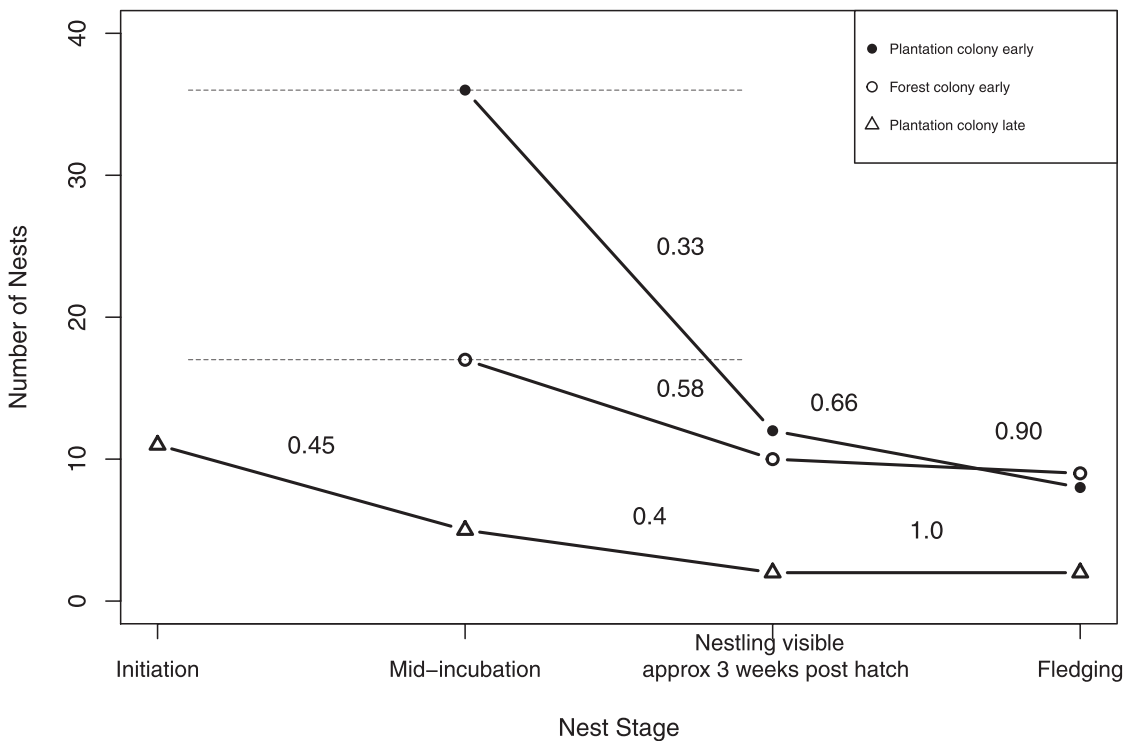


Figure 2. The number of nests and proportions of White-rumped Vulture nests (shown from the point from which they were monitored) that survived from one nesting stage to the next. Early nests are bound by intervals (broken lines) within which they were likely to be discovered. As there were no nests initiated later in the forest colony, it is represented only by one line.

nests in the forest colony ($n = 9$). Six of the eight early nests discovered later in the season in the forest colony fledged one young each. Two of the 11 nests discovered later in the season in the plantation colony fledged one young each. One nest that was found later had clearly also been built later, because it had not been present during earlier nest searches in the plantation colony; thus, it was grouped together with the late nests (Fig. 1 in supplemental material).

Apparent nest success varied with nesting stage as well as site (Fig. 2). Because we could not differentiate between nests just before a nestling hatched and immediately after hatching, the increase in apparent nest success from the egg stage to the nestling stage is likely to be slightly lower than estimated here. Overall, 21.2% of occupied nests were successful in the plantation colony ($n = 47$) compared to 52.9% for the forest colony was ($n = 17$).

Nest-Site Selection. All nests at the plantation colony were constructed in coconut palm, while in the forest colony, they were built in *Terminalia* or *Mangifera* trees. Nest trees were taller and had greater girth at breast height (GBH) than their nearby unused counterparts in both colonies (permutation test: $P < 0.05$ for both sites). At both sites, unused trees were not only shorter than nest trees in absolute height, but were also shorter relative to trees in the vicinity (as measured by the proportion of taller trees in a 10-m radius) compared with used trees (permutation test: $P < 0.05$; Fig. 3, Table 2). None of the other measured variables differed between nest sites and unused comparison sites at either colony. These patterns were also supported by a logistic regression analysis (supplemental material).

Correlates of Nesting Success. The plantation and the forest colonies had 39 and 8 failed nests and 10 and 9 successful nests (i.e., nests where one young fledged), respectively. In the plantation colony, of a

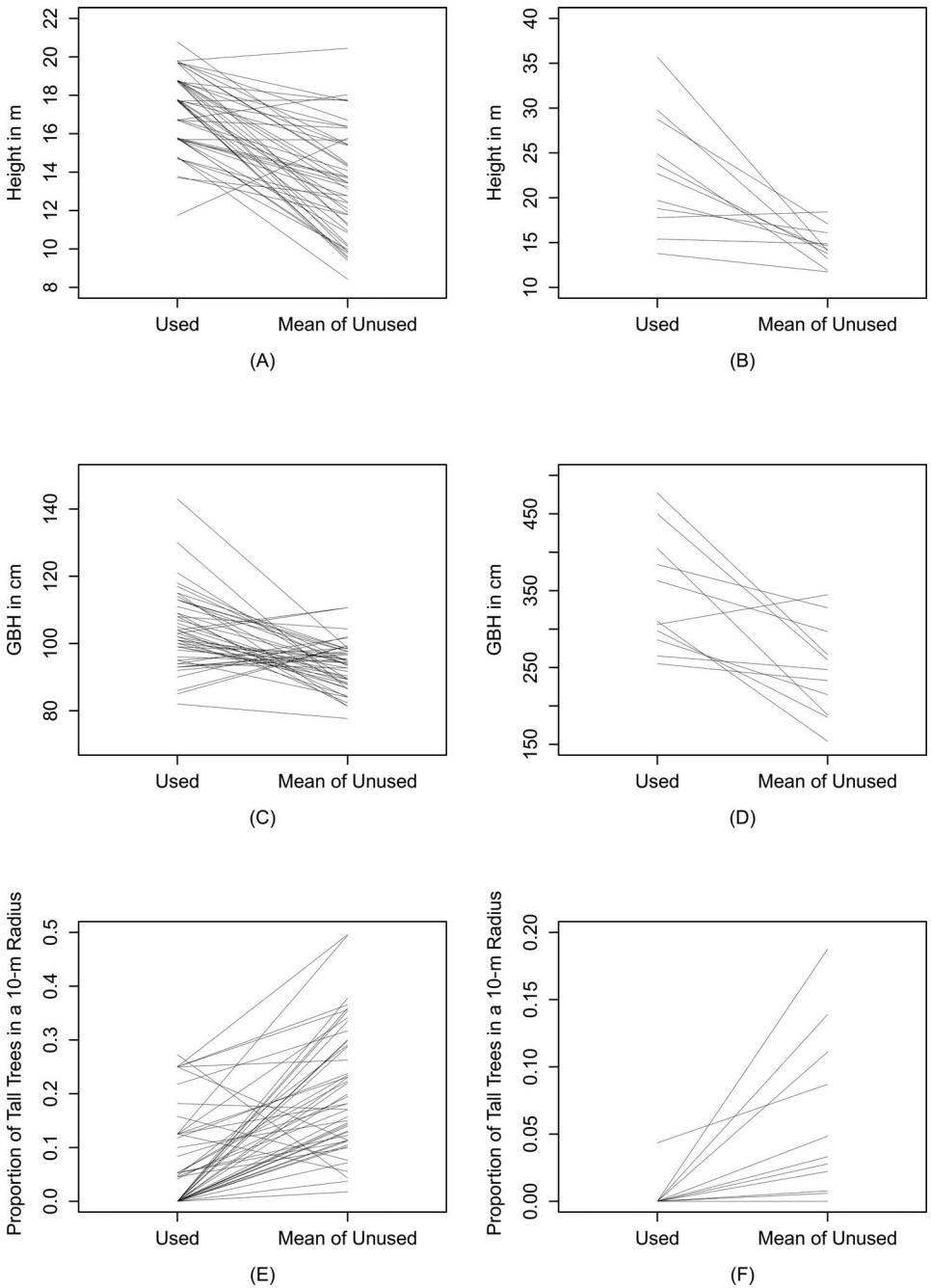


Figure 3. The relationship between heights (A and B), girth at breast height (GBH; C and D) and the proportions of tall trees in a 10-m radius (E and F) of matched used and (means of) unused trees the plantation colony (A, C, and E; $n = 48$ used trees) and the forest colony (B, D, and F; $n = 11$ used trees). The inclination of the lines joining each pair of points indicates the magnitude of difference between used and unused trees.

Table 2. Bootstrapped means and the 95% confidence intervals for the differences between used and (mean of) unused trees for nest-site variables at two colonies of White-rumped Vultures in India. Positive values indicate that the variable measured was higher in used than matched unused trees. See Table 1 for descriptions of variables.

NEST-SITE VARIABLE	COLONY	
	PLANTATION MEAN (95% CI)	FOREST MEAN (95% CI)
Tree height (m)	3.98 (3.15 to 4.80)	8.20 (4.42 to 12.30)
GBH (cm)	10.58 (6.70 to 14.44)	97.94 (49.39 to 146.34)
Lower canopy leaf count	1.49 (0.27 to 2.79)	—
Percent exposure	5.31 (1.30 to 9.43)	3.36 (−1.15 to 8.42)
Tree count at 10 m	4.28 (0.00 to 8.61)	−6.86 (−16.93 to 1.93)
Proportion of tall trees in a 10-m radius	−0.13 (−0.17 to −0.09)	−0.04 (−0.07 to −0.02)

total of 17 models we compared, there was no single top model (see supplemental material) and five models were ranked within a Δ AIC of 2.0 (Table 3). The model-averaged coefficient estimates across all models showed that the probability of successful nesting increased on taller trees and also on those with lower neighborhood tree density (Table 4). Using our model, we classified nests with a predicted success probability above 0.21 (i.e., the overall success rate observed in the study) as successful and all others as failed nests. Following this, the top five models, starting from lowest AIC value, correctly classified 66%, 62%, 54%, 64%, and 70% of a total of 48 nests compared to the simplified model (after dropping poorly predicting covariates from the global model), which classified only 33% of nests correctly. The forest colony had too few nests for us to detect any differences between successful and unsuccessful nests (Table 5).

DISCUSSION

The two WRV nesting colonies differed substantially in the number of nests as well as nesting success in the season we monitored them. Although the plantation colony had roughly three times the number of nests ($n = 49$) compared with the forest colony ($n = 17$), the plantation colony was not

necessarily better for breeding WRVs in this year. Both pre- and post-hatching nest survival were higher in the forest colony, but nest failure was higher at the pre-hatching stages than post-hatching for both colonies (Fig. 2). Similarly, in Nepal, the failure rate was higher during the incubation stage compared to the fledgling stage (Baral and Gautam 2007). Other factors, such as misidentification of nest stage, mock incubation (Anthony et al. 1994, Sahyadri Nisarga Mitra 2008), or infertile eggs could inflate our estimates of nest success, but are likely to be rare events.

Overall apparent success rates in the plantation colony (21.2%) was lower than most published nesting success rates after the year 2000 for WRV colonies in India, Nepal, and Pakistan, which range from 30% to 73% (Gilbert et al. 2002, Baral et al. 2005, Baral and Gautam 2007, Thakur and Narang 2012). However, success in Bangladesh between 2009 and 2011 was only 15.6% and 25.8% for multiple diclofenac-affected colonies together (Monirul and Khan 2013). Nesting success rate at the forest colony (53%) was relatively high, although sample size was small, and many nests were found during the nestling stage, which would tend to bias apparent nesting success higher. However, the published nesting success rates referenced here

Table 3. Best generalized linear models predicting the probability of successful nesting at the plantation colony, with associated parameters.

MODEL	Δ AIC	MODEL WEIGHT	df	LOG-LIKELIHOOD
Tree height + Tree count at 10 m	0	0.21	3	−20.52
Tree count at 10 m	1.36	0.1	2	−22.34
Tree height	1.68	0.09	2	−22.5
Tree count at 10 m + Distance to road	1.88	0.08	3	−21.46
Tree height + Tree count at 10 m + Distance to road	1.91	0.08	4	−20.29
Null	3.63	0.03	1	−24.564

Table 4. Coefficient estimates for predictors from all best generalized linear models used to predict probability of success for White-rumped Vulture nests at the plantation colony. Averaged coefficient estimates for all predictors are shown. (Refer to supplemental material for the list of all models.)

MODEL	AVERAGED ESTIMATES ACROSS ALL MODELS
	MEAN (SE)
Tree height	1.32 (0.49)
GBH	-0.41 (0.44)
Lower canopy leaf count	-0.27 (0.45)
Tree count at 10 m	-0.71 (0.27)
Proportion of tall trees in a 10-m radius	-0.45 (0.91)
Distance to road	0.56 (0.23)
Distance to nearest neighbor	0.66 (0.74)
Distance to house	-0.52 (0.27)
Distance to edge	0.09 (0.64)
Distance to construction	-0.34 (0.7)

describe multiple nesting colonies examined together, and thus they have larger sample sizes and are less likely to be extreme than those of small individual colonies, as we monitored.

As a consequence of the differential nest survival between the plantation and the forest colony, the number of young fledged per colony was comparable (10 for the former and 9 for the latter). High mortality in the plantation colony may be due to a limited number of high-quality nest sites (as in the case of Bearded Vultures [*Gypaetus barbatus*] in Spain; Carrete et al. 2006), and consequently, individuals nesting in lower-quality sites might suffer greater nest losses. Higher-quality individuals also may choose the most productive location (e.g., the forest), leaving the suboptimal plantation for poor-

er-quality individuals (Liberatori and Penteriani 2001).

Interference by potential predators like kites (*Milvus* spp.) and crows (*Corvus* spp.) was also more likely in the plantation colony, as these birds are commensal with humans, and such interference may have led to lower success. Crow attacks on nests were observed on several occasions (I. Majgaonkar unpubl. data), and such attacks may lead to higher mortality in absence of adults or via reduced incubation time (Arroyo and Razin 2006, Baral and Gautam 2007, Thakur and Narang 2012). Human persecution is unlikely the cause of low nest success, due to ongoing frequent monitoring by conservation organizations at the plantation colony. Similarly, nests in the forest colony were not near human habitation and did not pose any apparent threat or inconvenience to human health or livelihood.

Across India, the major reason for mortality in *Gyps* vulture colonies, especially before the nationwide ban on veterinary diclofenac, has been death induced by diclofenac consumption (Taggart et al. 2007, Cuthbert et al. 2011). In our study, we observed no symptoms of poisoning (e.g., drooping heads followed by death), and we neither found nor received information on dead WRVs in the area. However, it is possible that individuals died undetected while foraging away from the nesting colonies. Adults feeding young with contaminated meat might also result in nest failure. Although WRVs at both sites likely had overlapping foraging ranges, those at the plantation colony could have had greater access to domestic cattle carcasses due to higher human density, and subsequent diclofenac poisoning may explain lowered nesting success at the plantation. Although we offer these explanations as possibilities, we reiterate that no direct or indirect evidence of diclofenac poisoning was found.

Table 5. Nest-site variables for successful and unsuccessful nests of White-rumped Vultures at a forest colony in India. Confidence intervals are the 95% confidence limits of the bootstrapped means.

NEST-SITE VARIABLE	SUCCESSFUL NESTS	FAILED NESTS
	MEAN (95% CI) <i>n</i> = 9	MEAN (95% CI) <i>n</i> = 8
Tree height (m)	25.4 (21.1 to 29.8)	22.3 (18.1 to 27.4)
Girth at breast height(cm)	351.7 (301.3 to 411.0)	356.6 (313.9 to 402.0)
Percent exposure	15.8 (7.5 to 28.9)	17.8 (11.1 to 25.9)
Tree count at 10 m	35.8 (29.6 to 40.6)	33.9 (23.1 to 45.1)
Proportion of tall trees in a 10-m radius	0.00 (0.00 to 0.00)	0.01 (0.00 to 0.02)
Distance to nearest neighbor (m)	22.5 (3.3 to 56.4)	12.3 (1.9 to 26.6)
Distance to house (m)	173.2 (119.4 to 248.6)	144.2 (85.1 to 205.6)

At both colonies, WRVs chose to nest on trees that were taller in their immediate surroundings than unused trees. Taller trees may provide a better vantage point (Jackson et al. 2008) and may also be safer from terrestrial predators. Because WRVs nested only on two species (*Terminalia* and *Mangifera*) at the forest colony, this could be an artifact of the greater height and girth of these two species in the forest area, rather than selection for the species themselves. However, there was a clear selection for coconut palms in the plantation colony irrespective of the presence of *Sterculia* and *Mangifera* trees that were as large as the chosen nest trees at the forest colony. Interestingly, Thakur and Narang (2012) also found WRVs selected only one species, chir pines (*Pinus roxburghii*), in nesting colonies in Himachal Pradesh.

Although tree count in the surrounding area did not seem to influence nest-site selection (Table 2) in the plantation colony, among the potential nest trees, successful nests were in less dense plots and in marginally taller trees than failed nests (Tables 3, 4). Although successful nests were also distant from roads, they were sometimes found closer to inhabited houses and showed no preference for distance to smaller construction sites. We suggest that WRVs in this site were tolerant of such “passive” disturbances, and indeed, we know that large numbers nested successfully in trees along extremely busy streets of large cities in the past (Pain et al. 2003). This implies that the individuals in these sites may not be very sensitive to low-level disturbances, although it does not rule out potential negative effects of prolonged disturbances (Arroyo and Razin 2006).

The long-term consequences of low nest success depend on the proximate mechanisms by which WRVs choose nesting sites. If the plantation habitat has an inherent attraction for nesting individuals, but other factors render the habitat unfavorable (i.e., an ecological trap; Schlaepfer et al. 2002), then the future for WRVs in this region appears dim unless conservation interventions can minimize identified causes of nest mortality. Conversely, it is possible that WRVs show fidelity to their natal habitat, as suggested by a study of Egyptian Vultures (*Neophron percnopterus*; Meyburg et al. 2004). In the long term, such a mechanism limits population decline, because habitats that are more productive will receive increasing numbers of breeding individuals that return to their natal area to breed, and less-productive habitats may eventually cease to be used

for nesting. The current high use of the plantation colony for nesting may be a remnant of earlier conditions, when WRVs were predominantly nesting on Australian pines (*Casuarina equisetifolia*; Sahyadri Nisarga Mitra pers. comm.), which were extensively logged, possibly causing nesting to shift to coconut trees.

The above factors illustrate the need to understand the precise reasons for nest failure as well as the mechanisms WRVs use to choose nesting locations, at different scales. Both of these pieces of information will be necessary for effective conservation management of this critically endangered species.

SUPPLEMENTAL MATERIAL (available online): (1) Chart depicting nest counts from their discovery to either success or failure; (2) list of all models predicting probability of successful nesting at the plantation colony; and (3) list of all generalized linear models run to predict choice of nesting tree at the plantation colony, which were not presented in the published article because of space limitation and the extreme values of the estimates.

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Author contributions: IM, SQ, and CGRB conceived the idea and design of the study, and IM carried out the data collection. IM and SQ analyzed the data, and all authors were involved in writing. SQ and CGRB facilitated the study by providing equipment and resource people from whom guidance could be obtained.

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