First assessment of factors affecting the breeding success of two stork species in lowland Nepal using Bayesian Network models

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Abstract

Agricultural landscapes in south Asia have high human densities, experience year-round cropping, and the few remaining wetlands experience heavy human use. Factors affecting the breeding success of colonially-nesting waterbirds in such conditions are poorly understood. Using Bayesian Network (BN) models, we explored the importance of colony size, extent of persisting wetlands, human influence as proximity to habitation, and variation in landscape conditions due to changing crops (season) on the breeding success of two stork species – the Asian Openbill *Anastomus oscitans* and the Lesser Adjutant *Leptoptilos javanicus* – in lowland Nepal. Hypotheses were framed *a priori* to understand relative influences of each variable on breeding success, and to determine if heavily-used wetlands could ameliorate effects due to colony size and human presence. The model with all four covariates had best performance for both species, underscoring that complex combinations of factors affected stork breeding success in Nepal. In line with expectations, the importance of covariates differed between species. Proximity to human habitation and progression of season best explained breeding success for Asian Openbills, while season and the extent of wetlands around colonies best explained Lesser Adjutant breeding success. Wetland extent mediated some of the density-dependent effects, and also ameliorated effects linked to proximity to human habitation for both species, but had a weak ameliorating impact on season for both species. Analyses also highlighted considerable latency in models (> 49%) suggesting that additional aspects related to the dominant agriculture affect stork breeding success. Lowland Nepal's agricultural landscapes provide important ecosystem services in providing habitats that support successful breeding of the focal stork species, one of which is globally vulnerable. Retaining even heavily-used wetlands in such human-dominated areas will benefit waterbird breeding.

Key words: agricultural biodiversity, Asian Openbill, Bayesian Network modelling, Lesser Adjutant.

Persistence of colonially-nesting waterbirds in multi-cropped landscapes of Asia is poorly documented, and even less is known of how landscape conditions impact vital rates including breeding success (Subramanya 1996; Kushlan & Hafner 2000). Such information is urgently required to inform development plans being taken forward in countries such as Nepal and India, where recent studies have found a surprisingly high ability of agricultural landscapes to support bird diversity (Sundar & Subramanya 2010). Yet land use change and associated changes in traditional land management practices are already threatening habitats and species at landscape scales in north India, emphasising the need for a robust analysis of factors affecting bird populations (Sundar & Kittur 2012; Sundar *et al.* 2015). Agricultural areas in lowland Nepal are similarly experiencing development and land use change which threaten the persistence of bird species in this region, resulting in increased calls for research to inform management decisions (Inskipp *et al.* 2016; Sundar *et al.* 2016).

Studies of single- and multi-species waterbird colonies can be useful to measure features of landscape health, particularly as foraging and breeding grounds (Frederick & Collopy 1989; Frederick *et al.* 2009). When landscapes experience multiple human uses, land use composition (especially availability of wetlands and crops such as flooded rice) around colonies can influence both the number of colonies and individual breeding success, because of associated food resources for birds (Párejo & Sánchez-Guzmán 1999; Nowalski 2003; Tourenq *et al.* 2004). Breeding success can also be affected by colony-level characteristics such as colony size. Density dependent factors can result in lowered brood sizes in larger colonies (Shirai 2013), but this may be reversed if there is high habitat quality and food availability in the landscape (Jakubas 2005).

Little is known about factors affecting productivity at breeding colonies in landscapes with multiple cropping (*i.e.* more than one crop harvested per year), which are usually accompanied by strong seasonality and high human populations, especially when crops change with season as they do in lowland Nepal. In such landscapes, the time of breeding can be closely linked with specific farming activities and weather episodes that affect survival (Fasola *et al.* 2010). Human presence can have varying impacts on breeding success. In some areas, human disturbances targeted at colonies (*e.g.* cutting of nesting trees; collecting eggs and chicks for food) can reduce breeding success (Datta & Pal 1993; Fasola *et al.* 2010). In other areas, colony locations can be biased to trees located in human habitation (towns and villages), potentially due to protection afforded by people whose cultures favour coexistence with wild species (Subramanya 1996). Flooded rice paddies are known to enhance colony sizes and breeding success of some waterbird species (Fasola *et al.* 2010; Tourenq *et al.* 2004). However, the potential of persisting agricultural wetlands to help reduce adverse impacts attributable to human presence, or to altered landscape conditions caused by seasonal changes in crops, is poorly understood. In multi-cropped areas such as south Asia, wetlands are primarily maintained for human use, but still provide refugia to an impressive number of waterbird species and improve breeding success for a few species (Sundar 2009; Sundar & Kittur 2013). It is not clear, however, if heavily-used wetlands benefit the reproductive output of colonially-nesting species.

An array of factors, each having situation-dependent effects, seem to contribute to the ecology of waterbird colonies on agricultural landscapes. An exploration of the importance of relative and combined effects due to these factors on breeding success is needed to plan practical long-term conservation of colonially-nesting waterbird species on landscapes that experience multiple crops throughout the year. In this study, we therefore explored parts of Rupandehi and Kapilvastu districts of central, lowland Nepal, from August 2014 to January 2015, to document persistence of colonially-nesting waterbird species in the area. We found colonies of several species, most of which were single-species colonies of two stork species – the Asian Openbill *Anastomus oscitans* and Lesser Adjutant *Leptoptilos javanicus* (Koju 2015; Maharjan 2015; Sundar *et al.* 2016). Past studies on both species have provided information on breeding ecology (Asian Openbills – Datta & Pal 1993; Gopi & Pandav 2007; BirdLife International 2016; Lesser Adjutants – Baral 2005; Saikia 1995; Sharma 2006; Karki & Thapa 2013; Inskipp *et al.* 2016; BirdLife International 2017), but focused almost entirely on colonies located in wildlife reserves. Thus there is no definitive information on the ecological requirements of these two species when located in agricultural landscapes.

To understand the relative importance of factors affecting colony-level breeding success, we framed *a priori* hypotheses to match with a relatively small number of models to evaluate importance of individual covariates, and also to understand if wetlands around colonies could ameliorate potential negative effects due to colony-size, habitation and changing landscape conditions across seasons. We explored the strength of each hypothesis using Bayesian Network models, with analyses conducted separately for each species given differences in nesting periods, colony sizes, and diet. We framed the following three hypotheses:

1) *Variables and scales*: Breeding success at colonies will be a function of variables working at multiple scales, including the

colony (colony size), the landscape (extent of wetlands and human habitation around colonies), and time of breeding (a proxy for changing crops and landscape conditions). We also posited that associations with variables will differ by species, and specifically that wetlands will have a positive influence (particularly for the carnivorous Lesser Adjutant) and proximity to human habitation will have a negative influence on breeding success (particularly for the Asian Openbill). To evaluate this hypothesis, we required univariate models, one with each of the variables, and one full model with all four variables.

2) *Density dependence*: Larger colonies will experience lowered breeding success due to density-dependent effects (both species). Colony size effects will be, at least partially, reduced by increasing wetlands around colonies (particularly Lesser Adjutant) but not with increased human disturbance (especially the Asian Openbill that breed in larger colonies). Three competing models were required to assess this hypothesis: (i) a univariate model with colony size, and two additional models – (ii) colony size and wetlands, and (iii) colony size and human habitation.

3) *Season and wetlands*: Colonies initiated early, particularly those with chicks fledging during the monsoon (as with Asian Openbills), will have higher breeding success relative to those that were initiated later with chicks fledging when the landscape becomes drier (as with Lesser Adjutants), but colonies with more wetlands around them will fare better. This required two competing models to assess the hypothesis: (i) a univariate model with season, and (ii) one with both season and wetlands as explanatory variables.

Methods

Study area

Field work was carried out on parts of the adjacent districts of Rupandehi and Kapilvastu in central, lowland Nepal between August 2014 and January 2015 (Fig. 1a, b). Agriculture was the primary land use and the rest comprised woodlands, human habitation, wetlands (including marshes, village ponds, lakes, rivers), and scrublands (Koju 2015; Maharjan 2015). The following descriptions of farming practices and wetlands were based on field observations. Cropping patterns were influenced by three primary seasons – monsoon, winter and early summer – which had distinct precipitation and temperature regimes. The rainfall season or monsoon was from July to October, with average rainfall of 1,540 mm during this period, and with maximum temperatures varying between 33–35°C (Meteorological Forecasting Division data, accessible at http://www.mfd.gov.np/city?id=29). Flooded rice paddies were the primary crop in this season, with farmers flooding fields as early as June in preparation for the monsoon. Winter (November to February, rainfall averaged 57 mm for this period, and minimum monthly temperature varied between 8–11°C) was the season with the most diverse farming activity: rice harvest occurred in early winter followed by planting of wheat, mustard and potato as primary crops along with vegetables and fruits. Crops were harvested

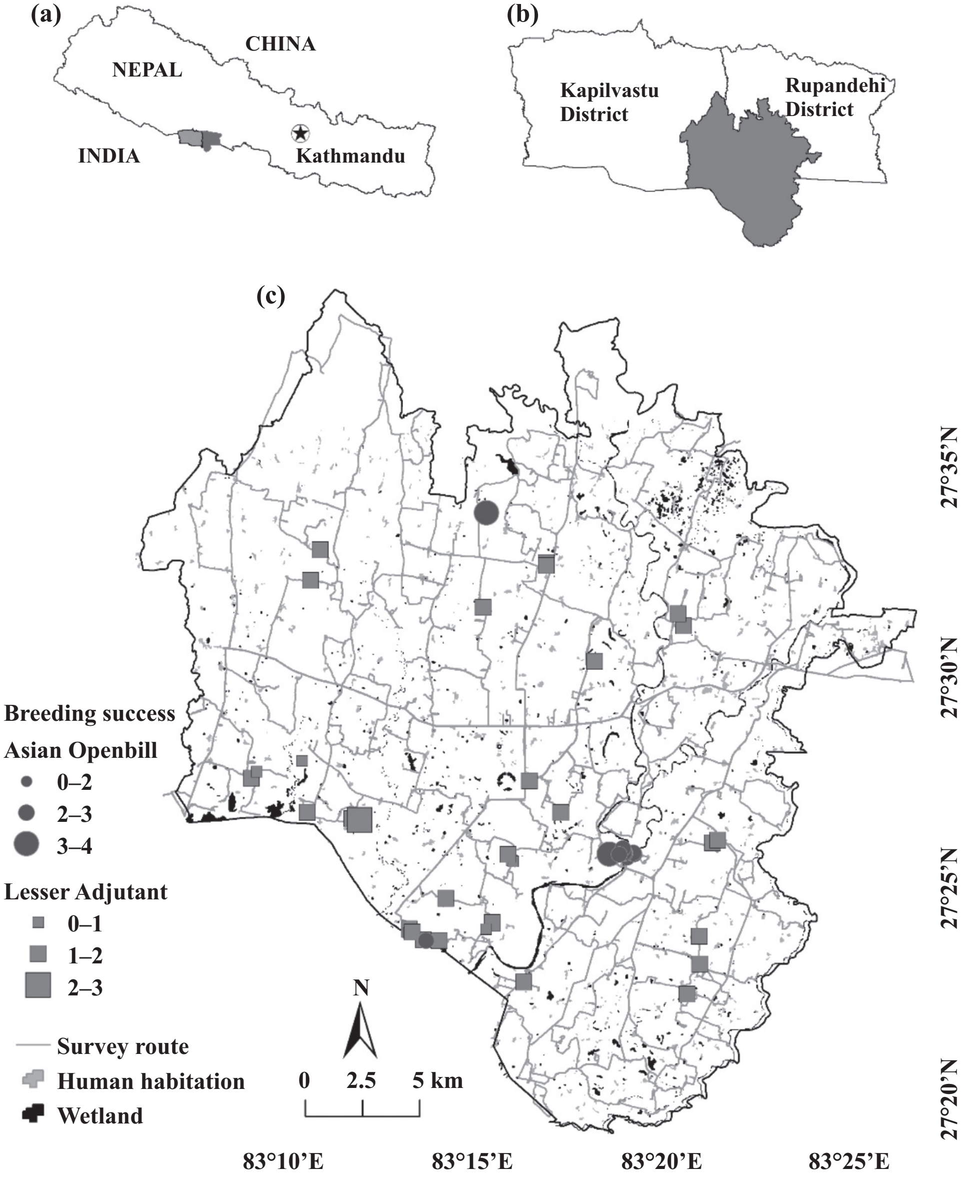

Figure 1. Location of the focal districts (a) and the study area (b) in lowland Nepal, with colonies of Asian Openbills and Lesser Adjutants in 2014 relative to the survey route, wetlands, and human habitation (c). Symbol sizes reflect colony-level breeding success (average number of chicks fledged per nest monitored at each colony).

in early summer (March to June) with the latter part of the season being too hot for crops (average high temperatures being > 40°C). Farmers and villagers used wetlands throughout the year for fisheries, grazing cattle and pigs, harvesting vegetation, and for watering crops. Wetland use by farmers increased greatly after the monsoon flooding, and nearly all the wetlands were seasonally flooded, drying up entirely during the summer, and with substantial inter-annual variation (K.S.G. Sundar & K.R. Gosai, pers. obs.). Trees comprised a combination of protected forests, orchards, clumps and individual trees in and around villages and crop fields, and shade trees along roads (Koju 2015).

Monitoring colonies and measuring breeding success

We inspected the most recent 1:25,000 topographic maps (National Geographic Information Infrastructure Project 1994) to identify roads accessible throughout the year, which would enable us to search for and monitor waterbird colonies between August 2014 and January 2015 (*i.e.* including the monsoon period), and used the road routes illustrated in Fig. 1c. At the time of the study, districts in Nepal were split into management units called Village Development Committees (or VDCs). To reduce spatial bias, we overlaid VDC boundaries over topographic maps and ensured that survey routes spanned the 48 VDCs (11 in Kapilvastu district and 37 in Rupandehi district) that were covered for this study (see Fig. 1). We interviewed villagers and farmers for locations of additional colonies away from survey routes. Although farmers helped to locate a few colonies away from roads, it is likely that our method provided data biased towards colonies located closer to habitation and roads. Survey routes were traversed at least once every two weeks to locate new colonies and to determine fates of nests in previously located colonies. Additional information on the surveys is available in earlier publications (Koju 2015; Maharjan 2015; Sundar *et al.* 2016).

We defined a colony either as nests on a single tree whose canopy was separated from other trees, or on a clump of trees that had a contiguous canopy, and colony size was the number of nests in each colony. We located 74 colonies of which 14 were of Asian Openbills, 35 of Lesser Adjutants, and 25 colonies of three other species (Cattle Egrets *Bubulcus ibis* (19), Pond Herons *Ardeola grayii* (4), and Red-necked Ibis *Pseudibis papillosa* (2); see Koju 2015). Breeding success was estimated at 13 Asian Openbill colonies (total nests recorded = 625; mean ± s.d colony size = 48 ± 51; range = 5–130 nests per colony), and at 35 Lesser Adjutant colonies (total nests recorded = 101; mean colony size = 2.9 ± 2.7; range = 1–13 nests per colony).

We estimated breeding success at the colony level as a fraction, as the total number of chicks observed fledging/total the number of nests monitored. Breeding success was thus measured as the mean number of fledglings per nest for each colony. Repeat visits to each colony, made every two weeks, were used to keep track of numbers of chicks surviving in each nest. Fates of all nests were tracked in small colonies, including all of the Lesser Adjutant colonies, and a sample of nests was monitored at larger Asian Openbill colonies where nests were often crowded or hidden from view. Asian Openbill chicks moved out of nests prior to fledging, and aggregated on nesting trees, making the outcome for particular nests difficult to ascertain in some cases. At smaller colonies of Asian Openbills, where numbers of chicks could be tracked before chicks began to move out of the nest, chick mortality occurred only when they were very young (storms and unknown reasons that potentially include predation and siblicide). No mortality was recorded of Lesser Adjutant chicks. All chicks of Asian Openbills that reached the age at which they moved away from the nest survived to fledging. At larger colonies, we counted chicks from a sample set of nests until the age just prior to their moving away, assuming that all of these chicks fledged successfully. We counted all chicks in all the nests of Lesser Adjutants.

On average, we recorded the fate of 62% (s.d. ± 32; range = 25–100%) of Asian Openbill nests per colony: 561 chicks fledged from 235 nests (average chicks fledged nest^{-1} = 2.39 ± 0.79; range = 0–4). Proportions of nests tracked decreased with increasing colony size (Pearson's correlation: $r_{13} = -0.76$, $P = 0.001$), but measured colony-level breeding success was poorly correlated to the numbers of nests tracked at each colony ($r_{13} = -0.058$, $P = 0.851$, n.s.) indicating that sample sizes did not systematically bias breeding success estimates. Fates of chicks were determined for all located nests of Lesser Adjutant: 162 chicks fledged from 101 nests (average chicks fledged nest^{-1} = 1.6 ± 0.78; range = 0–3).

Independent variables

To explore the influence of landscape content and context on reproductive output of colonially-nesting species in wetlands with heavy human use, we identified and quantified a variety of independent variables. Colony size was determined by three observers counting nests directly. Counts were made throughout the season to ensure that late nests were included in final counts. Observers walked around each nesting tree at a distance and counted all visible nests. At large colonies, observers also walked below the nesting trees to count nests hidden by the canopy. Counts were completed rapidly but carefully to minimise disturbance. There was no evidence of either species reusing nests for multiple clutches.

We used classified Landsat 8 satellite imageries (U.S. Geological Survey 2015) to measure the extent of broad land use classes of interest (crop fields or agricultural cultivation, human habitation, open lands, scrublands, wetlands) around colonies, from a cloud-free image corresponding to the end of the monsoon season (dated 27 October 2014). ERDAS Imagine* version 9.1 (Hexagon Geospatial 2006) software was used to pan-sharpen the image (using the "resolution merge" with "multiplicative and cubic convolution algorithm" functions), which gave a final pixel size of 15 × 15 m. Using a convergence threshold of 0.95, the image was subject to unsupervised classification (using the "Isodata algorithm" tool) to obtain 201 clusters, which were then designated into land use classes of interest. Pixels that were incorrectly classified when visually inspected using reference information (ground-truthing in the field and GoogleEarth images), were reclassified into their correct classes using on-screen digitisation with the Area of Interest (AOI) tool. The focal study area extended to 880 km^2 and classification showed that the different land uses of interest were dominated by crop fields (84%), while others were much rarer (tree cover = 6.9%; human habitation = 3.4%; open lands or uncultivable lands with minimal vegetation = 2.8%; wetlands, including marshes, lakes, ponds, and rivers = 2.5%; and scrublands = 0.4%). We tested for accuracy by assigning 20 random points for each class using the original pan-sharpened image as a reference image; the final classified image had an overall accuracy of 94.2%. Using ArcGIS* version10.2 (Environmental Systems Research Institute 2014) we generated a 5 km radius buffer around each colony and used it to measure extent of wetlands in km^2; this distance is within or slightly smaller than foraging distances recorded for storks elsewhere (Bryan & Coulter 1995; Paradis *et al.* 2004). The straight-line distance between colony locations and the edge of the nearest human habitation were measured on the classified image. Several colonies were located on trees within a human settlement, and the furthest was 860 m away (Fig. 1). We therefore used a 1 km buffer around each colony to obtain the extent of human habitation (in km^2) as a measure of human disturbance to that colony. We preferred a measurement of the extent of human habitation over distance to human habitation because habitations varied in size, and human disturbance was likely proportional to size of the settlement. Measures of the extent of wetlands and habitation were poorly correlated with each other for both species ($P > 0.15$, n.s.); given the lack of collinearity, both variables were retained for analyses.

Clutch initiation dates (*i.e.* the date on which the first egg was laid), estimated for each colony, were also included as an independent variable in the analyses. Several Lesser Adjutant colonies were initiated during the study, but some colonies of both species were active when observations commenced. A coarse estimate of chick age can be made from birds' plumage, and height relative to adult birds and behaviour. These measures were also recorded for both species during the multiple visits to the colonies (Maharjan 2015). On the basis of these observations, we subtracted the age of the oldest chick at first visit, and also the incubation period (average for Asian Openbill = 27 days, and Lesser Adjutant = 32 days; Gopi & Pandav 2007; Saikia 1995), to back-calculate the date of clutch initiation for each of the colonies. Given the variability in incubation periods and aging of chicks using field cues, we designated the estimated initiation date of the first nest in a colony to a calendar week. The earliest clutch was initiated during the week of July 14–20, so this was designated as week "1", whereas the last, initiated during the week of November 10–16, was designated as "18" (see Fig. 2).

Statistical analysis

We first checked for spatial autocorrelation for colony-level breeding success with

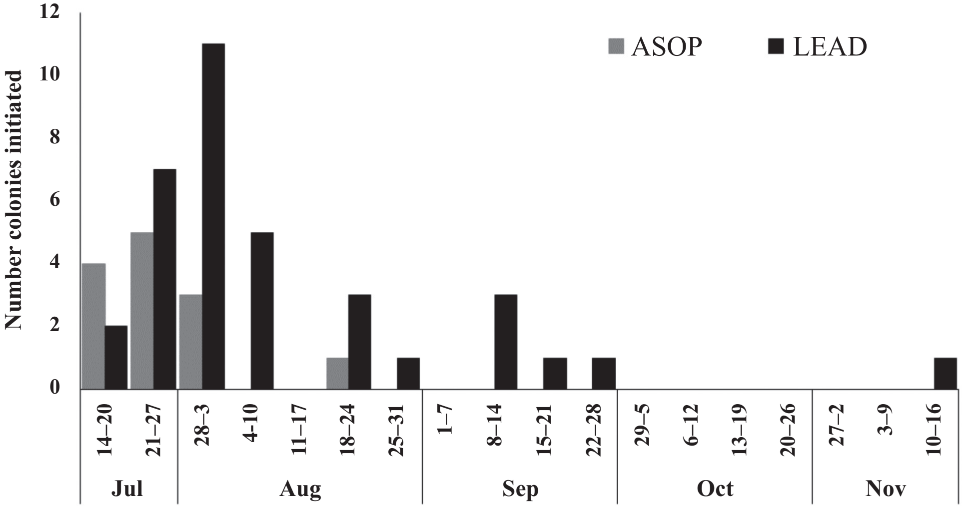

Figure 2. Chronology of initiation of colonies of two stork species (ASOP = Asian Openbill; LEAD = Lesser Adjutant) in lowland Nepal in 2014.

package "ape" in Program R (Paradis *et al.* 2004). Spatial autocorrelation was negligible for both species (Asian Openbill: Moran's I = –0.13; Lesser Adjutant: Moran's I = –0.06), and we did not include a spatial term in models for analyses. Analyses for each species were conducted separately because of their differing diets, colony sizes and nesting chronology. We first attempted analyses using frequentist methods by developing bivariate correlations of breeding success with individual covariates using linear regressions, and also non-parametric non-linear generalized additive models, to determine the direction of associations (Supporting Materials: Figs. S1–S5). As the response variable (breeding success) had a multi-modal distribution for Lesser Adjutant and data were relatively sparse for Asian Openbill (Figs. S1–S3), we used a Bayesian Network (BN) modelling approach that tends to be more robust to statistical assumptions that limit frequentist multivariate analyses. A full account of the frequentist approach with tests aiming to understand if wetlands around colonies could ameliorate potential negative effects due to colony-size, habitation and changing landscape conditions across seasons can be found in the online resource (Supporting Materials: Figs. S4, S5).

We chose BN models because they work well with small sample sizes where traditional, frequentist multivariate models must otherwise adhere to stricter conditions of larger sample size, data normality, and avoiding multicollinearity (Marcot 2012; Pawson *et al.* 2017) and have been shown to be a powerful tool in dynamic freshwater wetland systems (MacPherson *et al.* 2018). We explored the capacity of the covariates to explain breeding success by using Bayesian Network (BN) modelling with Program Netica® version 5.22 (Norsys Software Corp.

2015), following standard guidelines (Marcot 2012; Marcot *et al.* 2006). BN models represent relationships among variables with probabilities (Koski & Noble 2011).

We developed BN models for both stork species using breeding success as the response variable and environmental conditions as predictors (Table 1). The colony code was included as a nominal covariate in the Asian Openbill models to determine if potential, additional, latent (unmeasured) variables might account for unexplained variation of that species (which also had a small data set); we did not include colony code in the Lesser Adjutant models as there would be 35 nominal states for that variable that would render the sizes of the resulting conditional probability tables of the output node far larger than tenable with most entries unknown (Marcot 2012). We developed nine model variants for Asian Openbill (Table 2) and 16 variants for Lesser Adjutant (Table 3), using various subsets of the predictor variables. All continuous variables were discretized into four (Asian Openbill) or five (Lesser Adjutant) states using Netica's algorithm to specify state value boundaries that put approximately equal numbers of cases into each state. We used four states for Asian Openbill because of the smaller sample size of that species. The 16 Lesser Adjutant models included eight variants using five discretized states for the breeding success response variable that put approximately equal numbers of cases into each state, and eight variants using only two states representing zero (absence) and non-zero (presence) breeding success. None of the Asian Openbill colonies had zero breeding success, so we could not develop 2-state breeding success variants for that species.

Table 1. Variables used in the Bayesian Network models to identify variables important for breeding Asian Openbills and Lesser Adjutant Storks. [a] = Response variable used in the models. See text for explanation of methods.

Variable	Definition	Measure
Season	Calendar week of first egg laid	Ordinal count
Human habitation	Area of agricultural development within a 1 km radius of the colony	Km^2
Wetland	Area of wetland habitat within a 5 km radius of the colony	Km^2
Colony size	Number of nests monitored	Numeric count
Colony code	Unique name of each colony	Nominal code letter
Breeding success[a]	Mean number of storks fledged per monitored nest	Numeric count

Table 2. Covariates and complexity of Bayesian Network models of Asian Openbill colonies. See Table 1 for description of covariates. ^{a}X = variable included in the model; ^{b} = number of values of prior (*i.e.* marginal) and conditional probabilities.

	Covariate (predictor variable) sets used[a]					Response variable[a]	Bayesian Network model complexity		
Model no.	**Season**	**Human habitation**	**Wetland**	**Colony size**	**Colony code**	**Breeding success (4 levels)**	**No. nodes**	**No. links**	**No. probs.[b]**
1	X					X	2	1	20
2		X				X	2	1	20
3			X			X	2	1	20
4				X		X	2	1	20
5	X		X			X	3	3	84
6			X	X		X	3	3	84
7		X		X		X	3	3	84
8	X	X	X	X		X	5	7	212
9	X	X	X	X	X	X	6	9	888

We used the empirical case file databases on stork colonies to develop BN models to determine the relationships between prediction variables and the response variable, breeding success, measured as the proportion of chicks fledged in relation to the number of nests monitored at each colony. We used naive BN structures that depict the degree to which variation in the response variable is explained by each prediction variable. To develop the BN models, we employed a tree-augmented network (TAN) algorithm (Friedman *et al.* 1997) which is an advanced form of simple naive Bayes modelling that best accounts for explanatory power and that also identifies linkages between any of the prediction variables that are most dynamically related. The probability tables of the BN models were then parameterised using the expectation maximisation algorithm (Dempster *et al.* 1977; Marcot 2006), which is a convergent log-likelihood function that iteratively adjusts the probability values to maximise model fit.

We expressed the complexity and prediction accuracy of each model variant as follows. Complexity was measured as number of model nodes (variables), number of links (connections between the variables as identified with the TAN algorithm), and the total number of probability values in

Table 3. Variables and complexity of Bayesian Network models of Lesser Adjutant colonies. See Table 1 for description of variables. ^{a}X = denotes variable included in the model; ^{b} = number of values of prior (*i.e.* marginal) and conditional probabilities.

	Covariate (predictor variable) sets used^a					**Response variable^a**	**Model complexity**		
Model no.	**Season**	**Human habitation**	**Wetland**	**Colony size**	**Breeding success (5 levels)**	**Breeding success (presence/absence)**	**No. nodes**	**No. links**	**No. probs.^{b}**
1	X				X		2	1	30
2		X			X		2	1	30
3			X		X		2	1	30
4				X	X		2	1	30
5	X		X		X		3	3	155
6			X	X	X		3	3	155
7		X		X	X		3	3	155
8	X	X	X	X	X		5	7	405
9	X					X	2	1	12
10		X				X	2	1	12
11			X			X	2	1	12
12				X		X	2	1	12
13	X		X			X	3	3	62
14			X	X		X	3	3	62
15		X		X		X	3	3	62
16	X	X	X	X		X	5	7	162

the model (comprising both marginal and conditional probabilities). Prediction accuracy was measured by testing each model against the data sets to determine the rate of correctly predicting the breeding success state for each case as the dominant predicted probability outcome. Testing a model against the data used to build it is essentially calibration, not validation (Marcot 2006); we did not have independent data on stork colonies, nor data sets large enough to split, by which to do cross-validation. Calibration accuracy was measured using several indices: overall confusion error rate (percent of all cases incorrectly predicted), further split into Type I (false positive) and Type II (false negative) error rates; and performance indices of logarithmic loss, quadratic loss, and spherical payoff which are complementary measures sensitive to mean probabilities averaged over all states, mean probabilities averaged over all cases, and predicted probabilities of all states, respectively (Marcot 2006). Depending on model structure, these three performance indices can be uncorrelated, which is why we included all three. We calculated Type I errors as the proportion of cases predicted to be greater than the lowest breeding success state whereas the actual outcome was that lowest state, and Type II errors as the proportion of cases predicted to be the lowest breeding success state whereas the actual outcome was greater.

We then identified, for each species, the best models as those with low complexity, low confusion error rates, and best performance index values. These criteria served to balance model complexity with model (calibration) accuracy. We also determined the sensitivity structure of the best models using variance reduction and normalised percent variance reduction, which are quantitative measures of the independent degree of influence of each covariate on the response variable and commonly used in BN modelling (Marcot *et al.* 2006). The results of model calibration performance revealed the overall capacity of the covariates to explain breeding success of each species, and sensitivity analyses revealed the relative explanatory power (or uncertainty) of each covariate.

First, we identified the best BN models based on a balance of complexity and performance. Because all models had ≤ 5 covariates, none of the models was particularly complex (Tables 2, 3). With one exception, all models had ≤ 5 nodes, ≤ 7 links, and ≤ 405 total probability values, with the largest conditional probability tables in several of the Lesser Adjutant models containing 125 probability values, and most models having ≤ 155 total probability values. The one exception – Asian Openbill Model 9, Table 2 – included colony code as a covariate, discussed further below. Many BN models in other studies constructed empirically from case files using methods similar to ours are far more complex, such as ones developed to determine age class of martens (*Martes* sp.) that all consisted of > 1,000 total probability values (Pauli *et al.* 2011). Complexity was therefore not a limiting criterion for our model variants. Despite the care we have taken to reflect the limitations of the data and have presented several indices and tools to underscore the robustness of the results, we suggest that the analyses be considered preliminary in that the information is from a single season and from one location in lowland Nepal.

Results

BN Model performance

In our assessment of calibration performance of the Asian Openbill models (Table 4 and Supporting Materials Table S1), excluding Model 9 (explained below), overall confusion error ranged from 8–54%, Type I error ranged from 10–31%, and Type II error ranged from 0–50%, collectively

Table 4. Calibration performance outcome of Bayesian Network models of colony-level breeding success of Asian Openbills and Lesser Adjutants. See Tables 2 and 3 for covariates used in each model.

Model no.	**Overall confusion error %**	**Type I error (false presence) %**	**Type II error (false absence) %**	**Logarithmic loss index [0,infinity], 0 = best model**	**Quadratic loss index [0,2], 0 = best model**	**Spherical payoff index [0,1], 1 = best model**
Asian Openbill – Breeding success with 4 levels						
1	46%	31%	0%	0.874	0.541	0.668
2	46%	22%	50%	0.893	0.564	0.658
3	54%	31%	0%	1.000	0.615	0.619
4	31%	20%	33%	0.614	0.397	0.763
5	38%	31%	0%	0.614	0.410	0.754
6	31%	20%	33%	0.467	0.308	0.812
7	23%	20%	33%	0.360	0.256	0.851
8	8%	10%	0%	0.107	0.077	0.955
9	0%	0%	0%	0.000	0.000	1.000
Lesser Adjutant – Breeding success with 5 levels						
1	51%	7%	63%	1.1800	0.6158	0.6013
2	51%	14%	0%	1.2160	0.6330	0.5876
3	51%	10%	67%	1.2220	0.6571	0.5836
4	46%	14%	0%	1.0810	0.6033	0.6257
5	37%	6%	25%	0.6146	0.4002	0.7573
6	29%	9%	50%	0.5204	0.3430	0.7965
7	29%	11%	0%	0.5054	0.3431	0.8001
8	11%	3%	20%	0.1590	0.1152	0.9322
Lesser Adjutant – Breeding Success zero or non-zero						
9	14%	14%	0%	0.3290	0.2081	0.8847
10	14%	14%	0%	0.3920	0.2389	0.8711
11	14%	14%	0%	0.3315	0.2151	0.8806
12	14%	14%	0%	0.3214	0.2123	0.8815
13	9%	6%	25%	0.1518	0.1095	0.9375
14	14%	14%	0%	0.2526	0.1762	0.8989
15	11%	11%	0%	0.2377	0.1619	0.9085
16	3%	3%	0%	0.0673	0.0418	0.9775

identifying Model 8 as having the overall highest calibration accuracy and thus the best performing model. Values of logarithmic loss, quadratic loss, and spherical payoff indices all also pointed to Model 8, which included all four independent variables, as the best performing model (Fig. 3).

Calibration performance of the Lesser Adjutant models using five levels for breeding success (Table 4) similarly identified Model 8 as the best performing model, also with all four variables included (Fig. 4a). Although lower levels of Type II error were achieved with three other models, those models incurred much higher rates of Type I error and overall confusion error. Calibration performance of models using two levels for Lesser Adjutant breeding success indicated that the most inclusive Model 16 (with all four variables included), was the best performing model (Fig. 4b). However, sensitivity analyses of models using two levels showed poor performance with only 13% of the variance reduction achieved by all four variables (Table 5, Table S2). We therefore refer only to models using five levels for breeding success in subsequent discussions.

Including colony code as a nominal variable to the Asian Openbill model (Model 9, Table 2) resulted in a perfect model fit with no error (Table 4). This signalled that the model was an overfit to the data. Colony code itself carries no

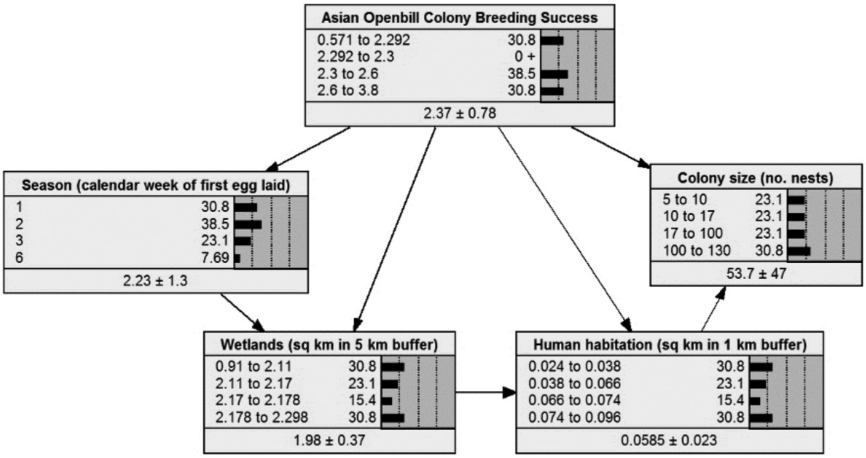

Figure 3. Best-performing Bayesian Network model of Asian Openbills (Model 8; see Table 4). The model, as structured from the empirical data, denotes nodes (variables) linked by their best explanatory relationships; because this is a naive Bayesian Network structure, arrows point from the output node (breeding success) to their covariates. Nodes are represented by discrete states shown as value ranges, each shown with a probability value, and nodes are linked with underlying conditional probabilities. Numbers at the bottom of each node are expected state values ± s.d.. As values of each covariate are specified for a particular stork colony, the probabilities of each state for breeding success are recalculated via Bayes theorem.

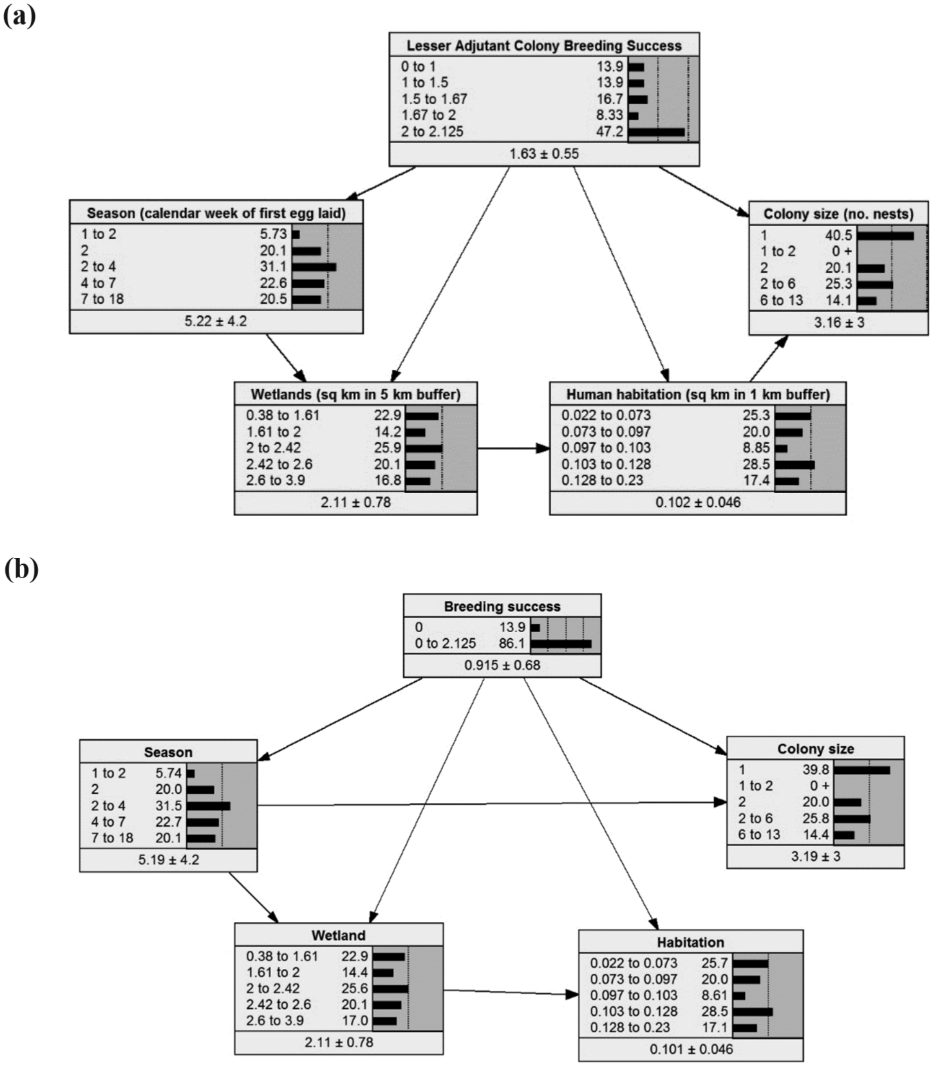

Figure 4. Best-performing Bayesian Network model of Lesser Adjutants (Model 8; see Table 5) with breeding success represented with five levels (a) and two levels (b). Further explanation as per Fig. 3.

environmental information, so the perfect fit resulting from including it also signals the presence of latent variables, indicating that there are environmental factors further explaining breeding success that were not measured. Latency is also apparent after conducting the sensitivity analyses, where the full complement of variables for both species explain 13–51% of the variance reduction (Table 5). Variance reduction is a measure of the degree to which a response variable is sensitive to the complement of

Table 5. Sensitivity analysis results of selected Bayesian Network models. See Tables 2 & 3 for model numbers.

Model	Variable	Variance reduction	Percent variance reduction
Asian Openbill Model 8	Human habitation	0.124	21%
	Season	0.093	16%
	Colony size	0.043	7%
	Wetland	0.041	7%
Lesser Adjutant Model 8	Season	0.053	17%
	Wetland	0.042	14%
	Human habitation	0.023	8%
	Colony size	0.003	1%
Lesser Adjutant Model 16	Season	0.020	4%
	Colony size	0.018	4%
	Wetland	0.016	4%
	Human habitation	0.003	1%

prediction variables; low values, *e.g.* < 50%, still imply some degree of sensitivity and thus explanatory power of the prediction variables but with some degree of variation still unexplained.

Hypotheses evaluation

Variables and scales hypothesis. Best-fit BN models for both stork species included all four covariates of season, human habitation, wetland, and colony size, confirming the hypothesis that breeding success of both species is affected by variables functioning at multiple spatial and temporal scales. The probability structures of the best-fit models for each species differed (Figs. 3, 4a, 4b), confirming that associations with variables differed by species. Additionally, sensitivity analyses indicated that breeding success of Asian Openbill was most sensitive to human habitation, whereas breeding success of Lesser Adjutant was most sensitive to wetlands (Table 5). Bivariate correlations showed that, in line with expectations, Asian Openbill breeding success declined with more human habitation around colonies (Fig. S4). However, contrary to expectations, Lesser Adjutant breeding success showed a negative correlation with increasing wetland extent around colonies (Fig. S5).

Density dependence hypothesis. Sensitivity to colony size alone was weak for both species relative to other variables (< 7%, Table 5). Bivariate relationships suggested weak negative effects on breeding success due to colony size for Asian Openbill in line with expectations, but a positive effect for Lesser Adjutant (Figs. S4, S5).

As hypothesised, breeding success of large Asian Openbill colonies did not seem adversely affected by the degree of human habitation if wetlands were available. For example, in the BN model (Fig. 3), when colony size was fixed to its highest state (100–130 nests) and wetlands fixed to its highest state (2.178–2.298 km^2), the expected value of breeding success was 2.445 ± 0.089 with the lowest amount of human habitation (0.024–0.038 km^2) and an equivalent 2.450 ± 0.087 with the highest amount of human habitation (0.074–0.096 km^2).

The hypothesised influence of wetland area mediating any density-dependence effects on breeding success rates of Lesser Adjutant was weakly supported by the BN models. For example, in the 5-state BN model (Fig. 4), when colony size was fixed to its highest state (6–13 nests) and human habitation was fixed to its highest state (0.128–0.23 km^2), the expected value of breeding success was 1.18 ± 0.75 with the lowest amount of wetlands (0.38–1.61 km^2) but 1.67 ± 0.14 with the highest amount of wetlands (2.6–3.9 km^2).

Season and wetland hypothesis. Minor support for the hypothesis was suggested by results of the sensitivity analyses of the best-performing models in which Asian Openbill breeding success was sensitive to season, whilst Lesser Adjutant breeding success was sensitive to season and also to wetland area (Table 5). Additionally, for both species, the model with both season and wetlands had better values of indices than the model with season alone, though model fits were not ideal and had fairly high level of errors (Table 4, Models 1, 5).

Parametrising the models for Asian Openbills, however, showed little variation in estimated breeding success when we changed states for season and wetlands from their lowest and highest values. For example, when season was fixed to its highest state (6), the expected value of breeding success was 3.2 ± 0.35 with the lowest amount of wetlands (0.91–2.11 km^2), and overlapped entirely with the estimated breeding success of 2.76 ± 0.74 with the highest amount of wetlands (2.178–2.298 km^2).

The data for Lesser Adjutants did not include case examples for specific outcomes of interest with which to parametrise the models, and we were unable to derive breeding success estimates to determine if wetlands ameliorated the impacts of season.

Discussion

The results of the study provide the first assessment of factors affecting colonially-nesting storks from an agricultural landscape in Asia, and is the first such study from lowland Nepal. Results showed that, for each species, the full model including all covariates (*i.e.* season, colony size, wetland area within 5 km of the colony, and area of human habitation with 1 km of the colony) was the model which best explained the variation in breeding success recorded during the study (Table 4). For Asian Openbills, the two most influential variables were habitation and season. While the variable "human habitation" had direct connotations of human-related disturbance, the variable "season" on the study landscape was more complex in including both variations in weather, and also human presence on the landscape due to year-long cropping activities. Lesser Adjutant breeding was affected by season and one environmental variable (wetlands; see Table 5). Stork breeding success in lowland Nepal is therefore likely to be impacted by alterations of landscape conditions, including both changes in extent of wetlands and also changes in the crops that in turn alter the timing and numbers of humans on the landscape. Despite being relatively rare, habitation and wetlands influenced stork breeding much more than variables at the colony level such as colony size. Analogous results were obtained in previous analyses of factors influencing foraging behaviours of these two stork species (Sundar *et al.* 2016) underscoring the strong influence of both habitat and human presence variables on stork breeding success.

In lowland Nepal, wetlands were rare and were heavily used by people throughout the year. Despite these characteristics, wetlands, particularly in association with other variables, positively influenced breeding success (this study) and the foraging behaviour of the two species (Sundar *et al.* 2016). In the neighbouring Indo-Gangetic floodplains, wetlands accounted for < 1% of the landscape and were much rarer than in Nepal, but positively influenced landscape-scale multi-season occupancy of Asian Openbills (Sundar & Kittur 2012). Their influence in ameliorating effects of habitation on breeding success, benefiting foraging success, and improving landscape-scale occupancy of large waterbirds points to their ecological benefits analogous to natural, relatively undisturbed wetlands (Frederick *et al.* 2009; Kelly *et al.* 2008). Further declines in wetland habitats in lowland Nepal therefore will be detrimental to stork persistence impacting both foraging and breeding ecology. It is not immediately clear why bivariate correlations show a negative association of Lesser Adjutant breeding success and wetlands around colonies, but unmeasured variables may be influencing the relationship between wetlands within 5 km of the colony and the birds' breeding success.

Colony size was only moderately positively related to breeding success (this study), and also to foraging behaviour of both stork species (Sundar *et al.* 2016). This result indirectly suggests that current densities and colony sizes of both species are at levels that are sustainable by the agricultural landscape of lowland Nepal. Lesser Adjutant colonies were a magnitude smaller than Asian Openbill colonies, and showed a slight improvement of breeding success in larger colonies contrary to expectations (see Figs. S4, S5). Waterbird colony size has been related to reduced breeding success due to predator effects and food depletion around colonies (Brunton 1999; Derdali *et al.* 2016). However, for large and potentially aggressive species such as Lesser Adjutants, it is likely that mortality due to predation is minimal and that larger colonies provided additional safety to nests and chicks. A specific study to investigate this unusual result would likely yield interesting results.

The number of Asian Openbill chicks fledged per nest in this study (2.39 ± 0.79 chicks per nest; $n = 235$ nests) was similar to that recorded in a protected mangrove reserve in eastern India (2.3, $n = 90$ nests, s.d. not available; estimated from Gopi & Pandav 2007). However, Lesser Adjutant breeding success per nest was significantly greater (unpaired t test: $t_{171} = 3.195$, $P < 0.01$; Cohen's d effect size = 0.49) in this study (1.62 ± 0.78, $n = 101$ nests) relative to observations in more forested areas in eastern Nepal (1.26 ± 0.66, $n = 73$ nests; estimated from Karki & Thapa 2013). Improved breeding success with increasing crops around colonies has been observed previously for various colonially-nesting waterbirds over both short- and long-term observations (Párejo *et al.* 1999; Tourenq *et al.* 2004). It appears that agriculture in lowland Nepal as currently practised with extensive flooding in one season, retaining small patches of more natural habitats such as wetlands amid crop fields, retaining patches of natural forests beside croplands, and retaining smaller tree patches on croplands for long periods, is a valuable multifunctional system. Agriculture here is providing food for humans and is also beneficial for large waterbirds. Understanding specific aspects of farmlands that benefit Lesser Adjutants will be greatly useful to develop an integrated agricultural policy in lowland Nepal. Comparable data from other landscapes dominated by agriculture are missing for both stork species. The dominant crops and cropping pattern (monsoonal rice and winter wheat) in lowland Nepal appear to be of high conservation value for the two focal stork species. Evidence was mixed as to whether season had a strong effect on breeding success, but the absence of a strong negative result suggests that a change to the current cropping pattern could affect the storks. Using non-linear frequentist modelling, Asian Openbills showed a decline in breeding success as season progressed, during which time the rice fields would become drier (Fig. S4). Despite a much larger data set for Lesser Adjutants, clear patterns linking season and breeding success were not apparent. Landscape conditions transitioned from flooded during the growth of the rice crop, to much more variable flooding during the winter to suit the greater diversity of crops. This included regular pulsed-flooding for wheat, to regular watering for some vegetables and fruits, to maintaining mostly dry conditions for some cereals and lentils. The varying landscape conditions therefore likely provides complexity that measurements made for this study captured inadequately.

A methodological caveat to the study is that, despite being the largest data set of its kind from south Asia with near-complete coverage of the focal study area with multiple visits to colonies, the robustness of BN models is weak due to overall data structure (*e.g.* missing case examples for specific outcomes in variables; highly clustered distribution especially of Asian Openbill colonies, see Fig. 1c), and small sample sizes. This was evident when setting the probabilities by use of the EM algorithm which, typically, often leaves "holes" in the probability tables, represented as uniform probability values, for combinations of variables not represented in the databases

(G. Sundar, unpubl. data). Although there is a risk of overfitting the models with small sample sizes, this can also lead to models underperforming for some combinations of covariate values. Model fits were evaluated explicitly via a range of metrics including both Type I and II errors, which led us to interpret results with much more caution than we would have using only indices listed in Table 4 that are analogous to measurements such as Akaike Information Criteria in frequentist methods (Arnold 2010). Such explicit evaluation is not commonly carried out using frequentist methods, and can provide conclusions that are not always based on statistical robustness.

BN models were, however, useful to test a small number of focused, *a priori* hypotheses and helped identify variables significant for stork breeding success. Models were also useful in revealing latency of > 49% (Table 5) suggesting that other variables, such as changes in prey availability and density in the changing crops, should be measured to provide a better understanding of factors driving stork breeding success on such complex agricultural landscapes. An improved dataset, perhaps with additional coverage of area or additional years, and measurements of additional variables relevant to stork breeding success, will be valuable for confirming and expanding on the results presented in this paper.

Conclusions

Past assertions that resident populations of these two stork species are rare in unprotected, agricultural areas of lowland Nepal (*e.g.* BirdLife International 2017) require updating. Our study discovered the largest known breeding populations of both species in Nepal, and both have high breeding success, comparable to or better than in areas that have fewer humans and are better protected. There are a growing number of narratives from Nepal that suggest that populations of both the focal stork species are being impacted negatively as a result of agricultural practices, and that the species (especially Lesser Adjutant) are declining (Inskipp *et al.* 2016). Our study has uncovered breeding populations of both species that have higher breeding success and number of breeding pairs than populations in more forested areas. These findings suggest that future explorations for these and other species with similar ecological requirements should explicitly include agricultural habitats. New observations can then be included in the models developed here, updating the probability tables and improving predictive accuracy. Additionally, always assuming that agriculture is detrimental to large waterbirds such as storks in status assessments is incorrect and, instead, we should be employing an evidence-based process that can reflect sound ecological information from a variety of settings where these species persist. Our observations therefore suggest that developmental planning in Nepal should not automatically assume that agricultural landscapes have low value for biodiversity, but that these landscapes can be beneficial to species such as storks. Many more basic studies covering the agricultural landscape of lowland Nepal are urgently necessary to help understand: (1) the species diversity supported, and (2) individual species' associations, especially population-level parameters, with these complex, multi-cropped areas.

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Photograph: Lesser Adjutant Stork at Kapilavastu, Nepal, by K.S. Gopi Sundar.

Photograph: Asian Openbill Stork at Kapilavastu, Nepal, by K.S. Gopi Sundar.