

Factors Affecting Provisioning Times of Two Stork Species in Lowland Nepal

Authors: K. S. Gopi Sundar, Bijay Maharjan, Roshila Koju, Swati Kittur, and Kamal Raj Gosai

Source: *Waterbirds*, 39(4) : 365-374

Published By: The Waterbird Society

URL: <https://doi.org/10.1675/063.039.0406>

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non-commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

Factors Affecting Provisioning Times of Two Stork Species in Lowland Nepal

K. S. GOPI SUNDAR^{1,2,*}, BIJAY MAHARJAN³, ROSHILA KOJU³, SWATI KITTUR² AND KAMAL RAJ GOSAI³

¹Program SarusScape, International Crane Foundation, E 11376, Shady Lane Road, Baraboo, Wisconsin, 53913, USA

²Cranes and Wetlands Programme, Nature Conservation Foundation, 3076/5, 4th Cross, Gokulam Park, Mysore, 570002, India

³Khwopa College, Department of Environmental Science, Dekocha, Changunarayan Road, Bhaktapur, 44800, Nepal

*Corresponding author; E-mail: gopi@savingcranes.org

Abstract.—The ecology of stork colonies in southern Asia are very poorly understood. Factors affecting provisioning times of adults were evaluated at nests of two stork species, the Asian Openbill (*Anastomus oscitans*) and the Lesser Adjutant (*Leptoptilos javanicus*), in lowland Nepal, where the landscape is dominated by multi-cropped agriculture fields. Analyses focused on understanding if provisioning times were influenced more due to colony-level variables, wetlands around colonies, or season. Using generalized additive mixed models and the information-theoretic approach, colony-level variables (brood size and chick age) showed non-trivial associations with provisioning times (substantially better than the null model). Univariate models with colony size and wetlands had poor support (worse than the null model). Season, which represented the changing cropping patterns, rainfall, and wetness on the landscape, was the most important variable for both species. The combination of season and wetlands was very important for provisioning Asian Openbills whose chicks fledged during the monsoon (July–October), but not for Lesser Adjutants whose chicks fledged in the drier winter months (November–February). Results strongly suggest that changing cropping patterns to a drier monsoonal crop, or reductions in wetland extents, will be detrimental to storks in Nepal. Received 9 April 2016, accepted 17 July 2016.

Key words.—agriculture, *Anastomus oscitans*, Asian Openbill, foraging, Kapilvastu, *Leptoptilos javanicus*, Lesser Adjutant, Nepal, Rupandehi.

Waterbirds 39(4): 365–374, 2016

The utility of landscapes dominated by crops for waterbird breeding and foraging is increasingly being recognized around the world. An increase in the extent of crops, such as rice cultivation, in association with additional factors, such as climate, prey availability and minimal human persecution, can facilitate population increases of waterbird species (Tourenq *et al.* 2004; Fasola *et al.* 2010; Sundar and Subramanya 2010; Sundar 2011). When crop fields occur in combination with other habitats, including human-modified and natural wetlands, mechanisms that facilitate persistence of waterbird populations can be complex. For example, several waterbird species, including herons, ibises and storks, show strong preferences for wetlands relative to rice fields as foraging and breeding habitats, particularly when conditions such as water depth and prey availability are favorable (Tourenq *et al.* 2001; Sundar 2006; Fidorra *et al.* 2015).

Waterbird foraging behaviors can be powerful indicators of the quality of landscapes and ecosystems. In natural wetlands, popu-

lation dynamics of colonial nesting species demonstrate strong relationships with foraging behavior, thus reflecting wetland quality (Frederick *et al.* 2009), as well as changing conditions during the nesting season (Bryan and Coulter 1995). Studies to test if strong and clear relationships exist between waterbird foraging behavior and habitat features in landscapes dominated by cultivation are relatively rare, but show similar relationships (Alonso *et al.* 2011). Such studies are extremely important to assess if waterbird behaviors that are relatively easy to observe could be used to understand quality of agricultural landscapes for waterbirds.

Provisioning at nests is one such easily observed behavior in colonial nesting waterbird species. Chick aggression seems unaffected by provisioning rates in herons, suggesting that adult birds provision at levels required to cater to the entire brood (Sullivan 1988). When adults cannot provide food at required levels, chicks use lower provisioning rates as a stimulus to switch to more profitable nests nearby (Redondo *et al.* 1995). Faster provi-

sioning, especially immediately after chicks hatch, were very important for nest survival in Great Blue Herons (*Ardea herodias*) (Auclair *et al.* 2015). While provisioning times can vary among individuals of a species, and between years, flight distances increased as the breeding season progressed, suggesting prey depletion in the nearest sites (Brzorad *et al.* 2015). In one experiment on storks, sites with supplementary foods had higher provisioning rates compared to sites without supplementary foods (Moritzi *et al.* 2001). Prey availability near breeding colonies was reflected by provisioning times, with birds shortening foraging trips considerably when prey was super-abundant (Anderson *et al.* 2005). Variations in prey availability caused strong variations in breeding success, including marked reductions in chick survival when prey became scarce (Anderson *et al.* 2007).

The majority of studies showcase the importance of larger-scale variables (habitat availability, progression of the nesting season), and that of a few colony-level variables (colony size, brood size, chick age). None, however, have tested the relative importance of both. We posited that relationships between the variables introduced above and provisioning times (time taken in minutes by adults to return to nests with food) at breeding colonies in agricultural landscapes should be similar to observations in protected wetland systems. We also tested the relative importance of larger-scale and colony-level variables for two stork species in an agricultural landscape in lowland Nepal.

Ecology of colonial nesting waterbirds, particularly storks, are very poorly known from Africa and Asia, and detailed studies at landscape scales focusing on specific aspects such as foraging ecology are exceedingly rare (e.g., Kalam and Urfi 2007). In this paper, we focus on understanding factors that affect provisioning times in two stork species, the Asian Openbill (*Anastomus oscitans*) and the Lesser Adjutant (*Leptoptilos javanicus*). Asian Openbills characteristically nest in large colonies, feed largely on snails, and forage in multiple habitats, including natural wetlands, irrigation canals, and agricul-

tural fields (Kahl 1971; Datta and Pal 1993; Sundar 2006). Conversely, Lesser Adjutants have very widely varying colony sizes, though never > 50 nests, and, until recently, were thought to breed exclusively in protected reserves with nesting trees located in or near large marshes (Hancock *et al.* 1992). The discovery of a number of colonies on trees located in rice paddies in Nepal underscores how little is known of this large stork species (Baral 2005; Sharma 2006; Karki and Thapa 2013). There is inadequate data to assess the global status of both stork species definitively, but available information has been used to classify Asian Openbills as “Least Concern” (BirdLife International 2012) and Lesser Adjutants as “Vulnerable” (BirdLife International 2013). This is the first detailed study of Asian Openbill and Lesser Adjutant requirements during the breeding season, and an exploration of how they fare in agricultural landscapes.

We were interested to understand how provisioning times of the two species were related to larger-scale variables (extent of foraging habitat around colonies), one temporal variable (progression of the nesting season), and three colony-level variables (colony size; brood size; chick age). Our *a priori* hypotheses were that provisioning times would: 1) be influenced more by larger-scale and temporal variables relative to colony-level variables; 2) be inversely proportional to extents of wetlands, with more wetlands around colonies also reducing the impact of potential food depletion as the nesting season progressed; and 3) be related to colony size, progression of the nesting season and wetland availability, with the specific assumption that more wetlands around colonies would reduce impacts of larger colonies.

METHODS

Study Area

We conducted this study in the central lowlands of Nepal spanning parts of the two Districts of Kapilvastu and Rupandehi (Fig. 1A, 1B). Climatically, this area is very similar to the Gangetic floodplains with three distinct seasons (summer: March to June; monsoon,

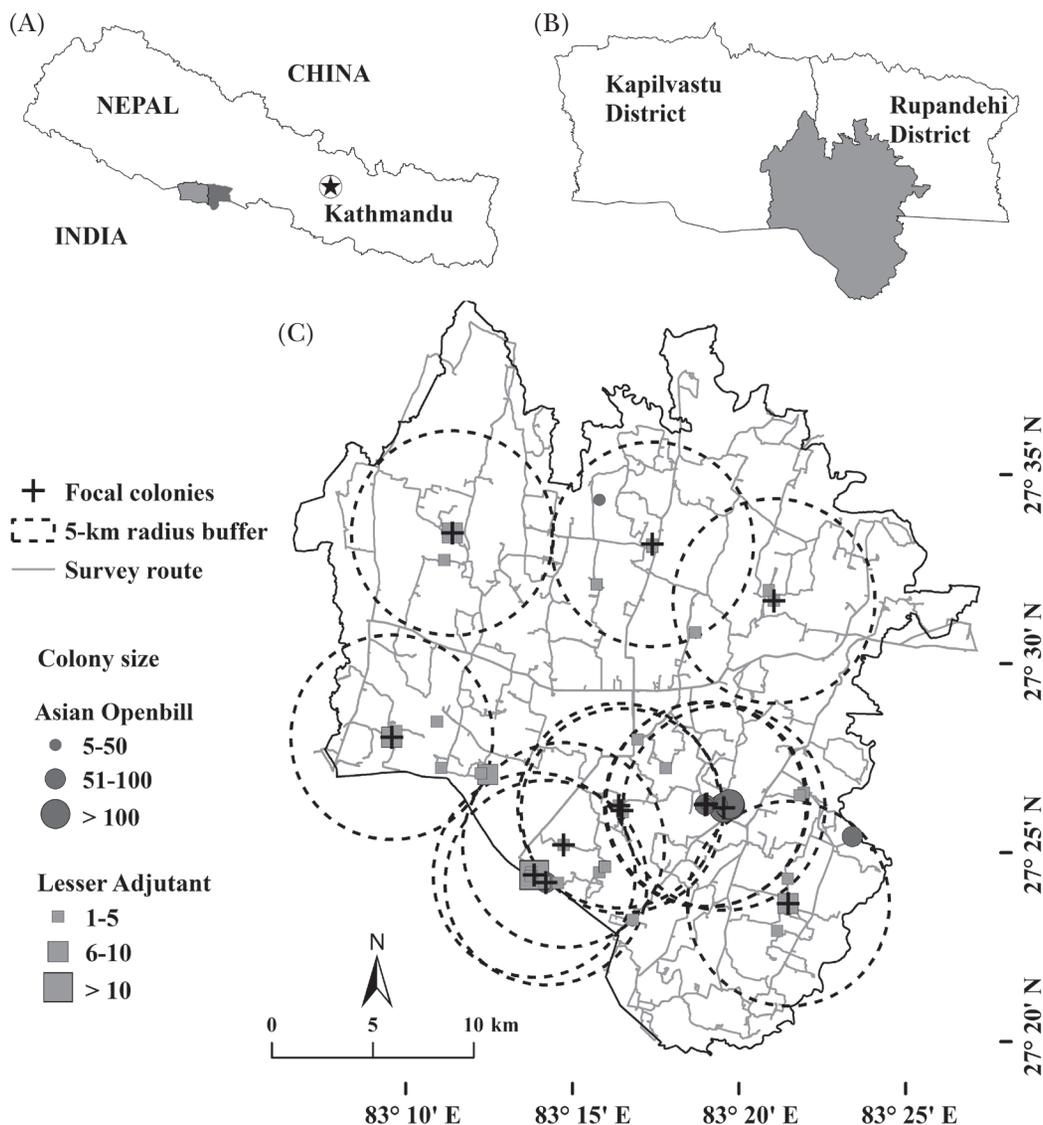


Figure 1. The study area showing: (A) the location of the two focal Districts in Nepal; (B) the location of the detailed study area (polygon) within Rupandehi and Kapilvastu Districts; and (C) survey route, locations and sizes of colonies of two stork species, and 5-km radius buffers drawn around focal colonies to measure availability of wetlands.

or rainy season: July to October; winter: November to February), the average temperatures varying between 12 °C to 42 °C, and seasonal rainfall with an annual average of approximately 1,200 mm. Agriculture is the dominant land use in the southern and central parts of both Districts (Kapilvastu: 60% of total area; Rupandehi: 74% of total area), with forests dominating the northern parts. Crops are planted to match the seasons, with flooded rice paddies during the monsoon followed by a combination of wheat and vegetables in the winter, and vegetables and fruits during the summer. Irrigation is largely rain-fed during the monsoon, and through artesian wells, bore wells and pumping from rivers and wetlands during the rest of the year.

Wetlands (foraging habitat) were very rare in both Districts, and there is no robust documentation of the actual extent of wetlands. Wetlands were a mixture of types including seasonal marshes, artificially constructed irrigation tanks, village ponds, oxbow lakes, and lakes. Small rivers and irrigation canals provided additional foraging habitats to storks. All wetlands and rivers experienced a very wide variety of human use, including harvest of wild vegetation, fishing, tuber collection, and grazing of cattle, pigs and goats (B. Maharjan and R. Koju, pers. obs.). Trees (nesting habitat) were scattered as fruit groves, roadside plantations, clumps retained inside and beside villages, and single trees in crop fields and villages (B. Maharjan and R. Koju, pers. obs.).

Field Methods

We used the extensive road network in the study area to conduct a preliminary survey in August 2014 and assess the presence of stork colonies (Fig. 1C). We also questioned farmers on locations of colonies that were not visible from the road. Several established colonies of Asian Openbills were located during the preliminary survey. We instituted regular behavioral observations at colonies and continued to monitor the road route on a fortnightly basis to locate new colonies as they were initiated. Lesser Adjutants commenced nesting in September 2014. Behavioral observations at colonies were continued until all chicks of both focal species had fledged in late January 2015. Analyses focused on behavioral observations made between September 2014 and January 2015.

We defined a colony as a group of storks nesting on a contiguous canopy that may have had more than one tree. Both focal species formed monospecific colonies. We located 14 Asian Openbill colonies (mean colony size = 52 ± 51 SD; Range = 5-130; median size = 19; total nests = 725) and 35 Lesser Adjutant colonies (mean colony size = 2.9 ± 2.7 SD; Range = 1-13; median size = 2; total nests = 101). For focal observations, we could only use four Asian Openbill colonies (colony size: Range = 21-130) that had newly hatched chicks when fieldwork commenced on 30 August 2014. We chose nine colonies of Lesser Adjutants (colony size: Range = 1-13) that encompassed all available colony sizes for this species.

Variable Descriptions

Provisioning time. The dependent variable was time taken by adult birds to return to nests to provision chicks and was measured by conducting focal-nest observations. For Asian Openbill colonies, two to three observers selected four to six observable nests from a vantage point at each siting. All nests were observable simultaneously in all of the focal Lesser Adjutant colonies. Observations were made from a distance ensuring that birds were not flushed. The time between the departure of an adult stork from the nest to its return was recorded in minutes. One adult usually remained at the nest ensuring that the measured time was the time taken for the adult to find prey and return to the nest where food was regurgitated (as with ingested food) or given to chicks (as with large prey like snakes). We discarded incomplete observations (departure or return time unknown), as well as observations when returning birds carried back nesting material, returned to roost and did not feed chicks, or when both adults departed from nests. For analyses, we retained only complete observations, which constituted 69% of all observations for the Asian Openbill ($n = 329$, total time = 8,766 min) and 54% for Lesser Adjutants ($n = 370$, total time = 14,472 min). Observations were carried out at colonies from sunrise to noon, or until birds that departed before noon returned, and were repeated fortnightly.

Colony size. The first independent variable was colony size. We walked around all trees with colonies and carefully included brief approaches to below the

canopy, and enumerated all nests once every fortnight. Three people conducted the counts each time to minimize the chance of nests being left out. While nesting at individual colonies was staggered, nests with fledged chicks were not reused by pairs nesting later in the season in both species. The highest number of nests counted at the end of the nesting for each colony (all or nearly all of the chicks had fledged) was used as colony size.

Brood size. We recorded the number of chicks in each focal nest during each observation period. Based on observed brood sizes of the two species (Asian Openbill: 1-4; Lesser Adjutant: 1-3) in nests that could be recognized by location, chicks did not seem to switch nests as seen occasionally with White Storks (*Ciconia ciconia*) (Redondo *et al.* 1995).

Chick age. We recorded behaviors across three broad age classes of stork chicks. Stage I included chicks that were barely visible from the ground, had only downy feathers on the head, were unable to stand for more than a few seconds, and did not reach the hock of adults when upright. Stage II included chicks that had near-complete replacement of head feathers, had nearly all downy feathers on wings, were able to stand but with very little wing flapping, and reached the wing feathers of adults when fully upright. Stage III included chicks that had very few down feathers and wing feathers in various stages of development, were exercising wings regularly, and were taller than wing-height of adults when upright.

Season. The progression of the nesting season from September 2014 to January 2015 was another variable of interest. The flooding of fields was reduced from late September onward in preparation for the ripening rice. Rice was harvested between late October and mid-November, and was replaced almost immediately with wheat and vegetables, leading to a drier and less homogenous landscape. Normally, the rainfall season is July-October, but during the study it continued erratically until February 2015. Consequently, we assumed that food availability changed for both species. We used the date of behavioral observations as a continuous variable, with "1" representing the first calendar date.

Wetlands and crop fields. We measured habitat (extent of wetlands and extent of crop fields) around each colony using a Landsat 8 (U.S. Geological Survey 2015) satellite image that covered the entire study area and was pan-sharpened using Erdas Imagine (Hexagon Geospatial 2006) to get a resolution of 15 x 15 m. We used an image from 27 October 2014, which was immediately after the rainfall season. The pan-sharpened image was subjected to unsupervised classification using the "Isodata algorithm" in Erdas Imagine with a convergence threshold of 0.95 to get 201 clusters. Each cluster was assigned to a broad land cover class. Incorrectly classified pixels were visually identified and re-coded using area of interest (AOI). Human habitation patches had signatures overlapping with fallow fields; we identified these on Google Earth and used on-screen digitization to create AOIs, which were then used to correct the image classification. The study area was spread across 880 km², and classified images yielded the following land use classes: crop fields (all crops; 84.0%),

tree cover (6.9%), human settlements (3.4%), open lands (uncultivable lands with no vegetation; 2.8%), wetlands (including marshes, lakes, ponds, and rivers; 2.5%), and scrublands (0.4%). An overall accuracy of 94.17% was achieved by assigning 20 random points for each class (total $n = 120$) and using the original pan-sharpened image as a reference image. We used a 5-km radius buffer around each focal colony to measure the area (in km^2) of two primary land uses (crop fields and wetlands) where storks were observed foraging during fieldwork. This buffer is within the range of, or smaller than, foraging distances of storks in other studies (Bryan and Coulter 1995; Herring *et al.* 2015). Both stork species likely altered foraging distances with the progression of the season due to changes in habitat and associated prey availability, as has been observed in heronry-nesting waterbirds elsewhere (Brzozard *et al.* 2015; Herring *et al.* 2015). However, we restricted our analyses to a one-time measurement of habitat availability using a conservative buffer size.

Food habits of the two focal stork species have not been studied in detail anywhere, but based on *ad hoc* observations of dietary items brought to the nests, diet overlap seemed minimal. More importantly, there was minimal overlap of the nesting season (Koju 2015; Maharjan 2015). Therefore, we have provided separate analyses for each species. Time of day potentially has an effect on foraging, and we reduced this bias by conducting observations before noon.

Analyses

We first assessed if variables at the colony level and extents of habitats were correlated. Colony size was not strongly correlated to average brood size in both species (Pearson's r , $P > 0.7$: Asian Openbill, $r = 0.19$; Lesser Adjutant, $r = 0.26$). Extent of wetlands around focal colonies was strongly and negatively correlated to extent of crop fields for both species ($P < 0.02$). We retained extent of wetlands for the analyses to allow testing of our *a priori* hypotheses. All analyses were conducted for each species separately.

We used a multi-model information-theoretic inference approach to test the relative strength of our hypothesis (Burnham and Anderson 2002). We used generalized additive mixed models (GAMM) for the analyses using package 'gamm4' (Wood and Scheipl 2014) in statistical program R (R Development Core Team 2015). GAMM is a non-parametric extension of the more commonly used generalized linear mixed models (GLMM), and are useful to fit models with data sets that are hierarchical and over-dispersed (Lin 1999; Zuur *et al.* 2009). They are particularly useful when the data are nested, and have strong non-linear fits with predictor variables. Since data collection was nested at the colony level with observations made at multiple nests in each colony, we used colony identity as the random variable. This also helped to avoid the assumption of no spatial autocorrelation in the data. We specified a Poisson distribution for all analyses, and avoided over-fitting by restricting the number of knots in smoothing splines (k) when range of values of explanatory variables was

small (brood size, $k = 3$ or 4 depending on the species; chick age, $k = 3$; colony size, $k =$ number of different sized colonies; wetland extent, $k =$ number of colonies since the measurements were restricted to focal colonies). We generated graphs for estimated smoothers with each individual variable for both stork species to visually assess the nature of fit and provide potential ecological reasons for the fits.

We ran the null model (only random intercept), five univariate models, and a full model with all five variables, as well as two additional models to match with our *a priori* hypotheses, for a total of nine models for each species. The coefficient for the random intercept was highly significant ($P < 0.01$) in all models, and smoothing terms were highly significant ($P < 0.01$) for nearly all variables (except for colony size in Asian Openbills and wetlands for both species) pointing to the suitability of GAMM for analyses. For models that converged, we generated Akaike Information Criterion (AIC) values with the statistical package R using the function 'model\$mer' in package 'gamm4' to compare between models (Wood and Scheipl 2014).

RESULTS

Provisioning times were, on average, lower for Asian Openbills ($\bar{x} = 26.59$, $SD = 32.92$) compared to Lesser Adjutants ($\bar{x} = 38.15$, $SD = 50$), with considerable variations in both species. GAMM-based model fits showed that provisioning times were weakly affected by wetland extent alone for both species, and had AIC values less than that of the null model for both species (Tables 1 and 2). For both species, associations of provisioning times with two colony-level variables (brood size and chick age) and season were considerably better than the null

Table 1. Model selection statistics (df = degrees of freedom of residuals; Δ AIC = difference in AIC values between the particular model and the model with the lowest AIC (10,140.9); Deviance = model deviance) for factors affecting provisioning times by adult birds at nests of Asian Openbills in lowland Nepal. (Models "Full" and "Wetlands + colony size + season" did not converge, and are not included in the Table.)

Model	df	Δ AIC	Deviance
Wetlands + season	336	0.0	10,130.9
Season	337	2.0	10,134.9
Chick age	338	759.6	10,894.5
Brood size	338	803.2	10,938.1
Null	339	866.3	11,003.2
Colony size	338	868.3	11,003.2
Wetlands	338	868.3	11,003.2

Table 2. Model selection statistics (df = degrees of freedom of residuals; Δ AIC = difference in AIC values between the particular model and the model with the lowest AIC (15,256); Deviance = model deviance) for factors affecting provisioning times by adult birds at nests of Lesser Adjutants in lowland Nepal. (Model "Full" included all five variables.)

Model	df	Δ AIC	Deviance
Full	371	0.0	15,236.0
Season	377	78.5	15,326.5
Wetlands + colony size + season	373	79.9	15,319.9
Wetlands + season	375	81.6	15,325.6
Chick age	378	1,045.5	16,295.5
Brood size	378	2,054.7	17,304.7
Null	379	2,100.5	17,352.5
Colony size	378	2,101.3	17,351.3
Wetlands	378	2,102.5	17,352.5

model, with season being the most important variable.

For Asian Openbills, the univariate model with season was considerably better than the next model (757 AIC units), and including wetlands improved the model marginally (two AIC units). Brood size had a non-linear association with provisioning time decreasing when brood sizes were > 3 (Fig. 2). Provisioning time increased nearly linearly with chick age. Provisioning time had a strongly non-linear association with season, increasing initially (early September) and then fluctuating about a mean until all chicks fledged in mid-October (Fig. 2).

For Lesser Adjutants, the top model included all the variables, and was considerably better than the next best model (Table 2). The next three models included season;

they were within four AIC units and were substantially better than the subsequent models with chick age and brood size (963 AIC units). However, models with chick age and brood size were greatly improved relative to the null model (45 AIC units). Provisioning time was highest for brood sizes of one, but declined and was similar for brood sizes of two or three, and increased almost linearly with chick age (Fig. 3). Provisioning time fluctuated as the season progressed, increasing greatly in late September and again in early to mid-December (Fig. 3).

DISCUSSION

Variables had strong non-linear associations with provisioning times, with a strong nested effect due to individual colonies, of both stork species, which underscores the value of using GAMMs. In line with our *a priori* hypotheses, most of the colony-level variables (brood size and chick age) were substantially better than the null model for both species. However, contrary to expectations, extent of wetlands around colonies did not greatly impact provisioning times of both stork species in lowland Nepal. Instead, season, which represented the changing cropping patterns and wetness on the landscape, had the highest effect of any single variable on provisioning times of both species. This was particularly evident with Lesser Adjutants (Fig. 3), which increased provisioning times in late September (as the rice began to

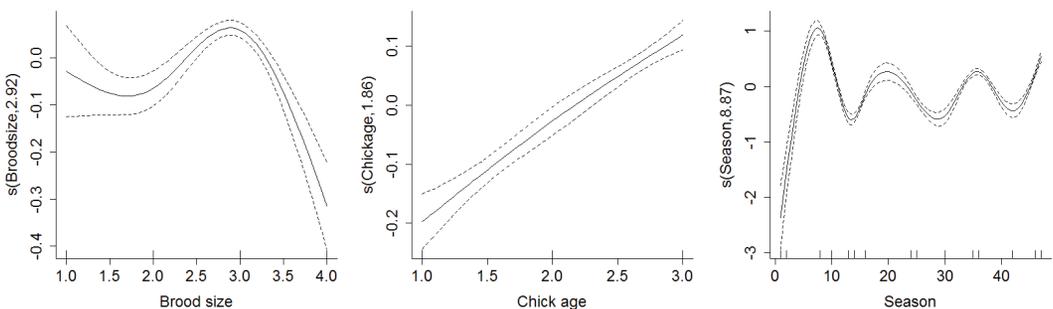


Figure 2. Estimated smoothers of provisioning times against individual variables (see x-axis labels) using generalized additive mixed models for Asian Openbills. All smoothers are centered around zero. Relationships with colony size and extent of wetlands were very weak and are not shown here. Season extends from 6 September to 22 October 2014 on the x-axis.

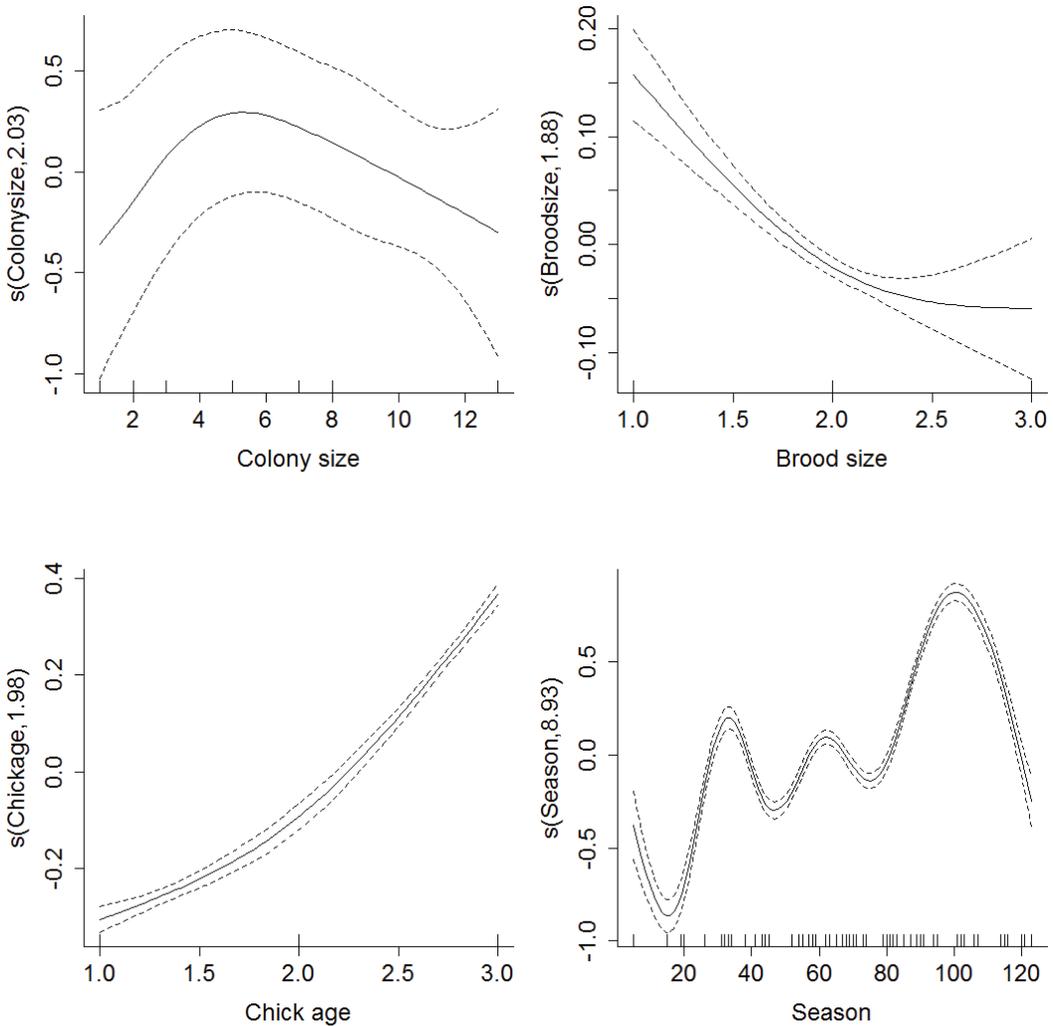


Figure 3. Estimated smoothers of provisioning times against individual variables (see x-axis labels) using generalized additive mixed models for Lesser Adjutants. All smoothers are centered around zero. Relationship with extent of wetlands was very weak and is not shown here. Season extends from 10 September 2014 to 7 January 2015 on the x-axis.

ripen) and in mid-December (when wheat planting had been entirely completed). It is likely that the dominance of farmlands overwhelmed the effects of wetlands, which constituted < 3% of the landscape. Also contrary to expectation, Lesser Adjutant provisioning times were most influenced by a combination of all the variables (Table 2), suggesting that studies that test habitat impacts in similar landscapes will need to control for colony-level and temporal variables.

There was strong support for hypothesis 2 for Asian Openbills; the most important model has wetlands and season, sug-

gesting that food from both wetlands and the flooded fields were important for this species. Asian Openbill nesting began during the early-monsoon season, and chicks had largely fledged before the monsoon ended, when both fields and wetlands were still flooded. These findings are analogous to observed habitat use by Asian Openbills in the India portion of the Gangetic floodplain, where they preferred wetlands and irrigation structures such as canals as foraging habitats (Sundar 2006). Asian Openbill occupancy of the landscape during the monsoons, when rice was the dominating crop,

was similarly very high (Sundar and Kittur 2012). The model with season and wetland for Lesser Adjutants, however, was a poorer fit than the model with season alone, suggesting poor support for hypothesis 2 for this species. Lesser Adjutant provisioning started toward the end of the monsoon season until late-winter, when wetlands were drying up and also facing increased human use, which would render wetlands less suitable as foraging habitats. Model selection therefore matched cropping patterns and human activity on the landscape, and also suggests that the farmlands are important foraging habitats for Lesser Adjutants. Results therefore suggest that: 1) deterioration of wetlands (condition or extent) on this landscape will affect stork (particularly Asian Openbill) provisioning times negatively; and 2) changes in cropping patterns can have dual impacts – they can affect stork behavior as well as accentuate the impact of wetland persistence or loss on stork foraging.

Colony size, surprisingly, had very little effect on provisioning times of both species in contrast to our hypothesis 3. Asian Openbills had a wide variability in colony sizes and Lesser Adjutants are large birds, which had led us to suspect that even modest increases in colony sizes would be reflected in provisioning times. This lack of effect is likely due in part to the small sample size of focal colonies, especially for Asian Openbills. A non-linear effect was visible for Lesser Adjutants, but the effect was weak relative to other variables. Results likely reflect the availability of adequate food on the landscape for both species at current population levels and observed colony sizes.

Provisioning times increased with chick age for both species. This was similar to other waterbirds when adult birds had the lowest provisioning times (or highest provisioning rates) immediately after chicks hatched (Auclair *et al.* 2015). Adults of both species also returned faster when nests had larger broods. This suggests that colony-level parameters cannot be ignored entirely in similar studies, and their importance relative to landscape-scale variables such as habitats need to be assessed simultaneously.

We were unable to document quality and size of food brought back by storks and assume that they remained similar throughout the nesting season. We also assumed that provisioning was highest in the mornings, and that storks did not alter feeding regimes throughout the season. These aspects require confirmation via the use of video equipment. In our study area, however, the risk of video cameras being stolen is high.

We were only able to include habitat measurements as a one-time measurement despite knowledge that the extent of crop fields and wetlands altered over the course of the study. We were also unable to assess prey availability, change in prey availability, and relationship of prey availability to daily rainfall as the season progressed. Few assessments have been made in this region of availability of stork prey in crop fields and non-protected wetlands in agricultural landscapes. Future studies can focus on these lesser-known aspects in combination with behavioral and population-related metrics.

One variable of potential interest for future studies is the proximity of colonies. It is likely that colonies clustered together deplete food much more rapidly relative to more dispersed colonies. We were unable to incorporate this aspect into our analyses since we did not have information on colonies present immediately outside of our study area.

Our study provides additional evidence of the utility of relatively simple behaviors, such as provisioning times of adults at nests, in colonial nesting waterbirds to assess potential impacts of habitats and agricultural practices. We also showcase the utility of GAMM in being very useful to work with non-linear associations between variables, and with nested data. Finally, we underscore the enormous ecological value of the agricultural landscapes in central, lowland Nepal in helping maintain significant populations of two stork species that were hitherto unknown. Lowland Nepal, like much of the neighboring plains of India, is geared to experience increased human populations and associated development (Inskipp *et al.* 2016). The study area surrounds the World Heri-

tage site of Lumbini, the birthplace of Lord Buddha, and there is growing concern that poorly planned development will damage the site both physically (e.g., via pollutants) and spiritually (via reducing the natural/traditional nature of the landscape) (Paudel *et al.* 2013). Our study provides new information to show that large-scale development plans that do not explicitly incorporate the ecological benefits of the agricultural landscape into planning processes will be deleterious to species such as storks.

ACKNOWLEDGMENTS

This project was conducted as part of the long-term monitoring effort of Program SarusScape established jointly by the Nature Conservation Foundation (NCF) and the International Crane Foundation (ICF). At NCF and ICF, KSGS and SK thank J. Langenberg, S. Prabhakaran, and N. Raj for administrative support. Fieldwork for this paper was conducted as part of BM's and RK's Master's theses in Environmental Science at Khwopa College; both are Nepali nationals and complied with national laws and rules for wildlife research as mandated for observational studies outside reserves by the Department of National Parks and Wildlife Conservation, Nepal. BM, RK, KSGS and KRG thank the Research Committee and R. Jayakhwo of Khwopa College for facilitating the thesis work. We thank Bhikku Vivekananda for literature on the Lumbini World Heritage Site. KSGS thanks the Arthur L. and Elaine V. Johnson Foundation, Polly and Bo Beal, Karen and Joseph Branch, the Bryan Guinness Foundation, ICF, Maggie Jones and David Linton for multi-year support to Program SarusScape. The manuscript was subject to ICF internal review prior to publication. We also thank two anonymous reviewers for helpful comments on an earlier draft.

LITERATURE CITED

- Alonso, J. C., J. A. Alonso and L. M. Carrascal. 2011. Habitat selection by foraging White Storks, *Ciconia ciconia*, during the breeding season. *Canadian Journal of Zoology* 69: 1957-1962.
- Anderson, S. K., D. D. Roby, D. E. Lyons and K. Collis. 2005. Factors affecting nest provisioning by Caspian Terns nesting in the Columbia River estuary. *Waterbirds* 28: 95-105.
- Anderson, S. K., D. D. Roby, D. E. Lyons and K. Collis. 2007. Relationship of Caspian tern foraging ecology to nesting success in the Columbia River estuary, Oregon, USA. *Estuarine, Coastal and Shelf Science* 73: 447-456.
- Auclair, M. M., K. A. Ono and N. G. Perlut. 2015. Brood provisioning and nest survival of *Ardea herodias* (Great Blue Heron) in Maine. *Northeastern Naturalist* 22: 307-317.
- Baral, H. S. 2005. Surveys for Lesser Adjutant *Leptoptilos javanicus* in and around Kosi Tappu Wildlife Reserve, Nepal. *Forktail* 21: 190-193.
- BirdLife International. 2012. *Anastomus oscitans*. The IUCN Red List of Threatened Species, v. 2012.1. <http://dx.doi.org/10.2305/IUCN.UK.2012-1.RLTS.T22697661A40232058.en>, accessed 1 December 2015.
- BirdLife International. 2013. *Leptoptilos javanicus*. The IUCN Red List of Threatened Species, v. 2013.2. <http://dx.doi.org/10.2305/IUCN.UK.2013-2.RLTS.T22697713A49015832.en>, accessed 1 December 2015.
- Bryan, A. L., Jr. and M. C. Coulter. 1995. Foraging strategies and energetic costs of foraging flights by breeding Wood Storks. *Condor* 97: 133-140.
- Brzorad, J. N., A. D. Maccarone and H. M. Stone. 2015. A telemetry-based study of Great Egret (*Ardea alba*) nest-attendance patterns, food-provisioning times, and foraging activity in Kansas, USA. *Waterbirds* 38: 162-172.
- Burnham, K. P. and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach, 2nd ed. Springer-Verlag, New York, New York.
- Datta, T. and B. C. Pal. 1993. The effect of human interference on the nesting of the openbill stork *Anastomus oscitans* at the Raiganj Wildlife Sanctuary, India. *Biological Conservation* 64: 149-154.
- Fasola, M., D. Rubolini, E. Merli, E. Boncampagni and U. Bressan. 2010. Long-term trend of heron and egret populations in Italy, and the effects of climate, human-induced mortality, and habitat on population dynamics. *Population Ecology* 52: 59-72.
- Fidorra, J. C., P. C. Frederick, D. C. Evers and K. D. Meyer. 2015. Selection of human-influenced and natural wetlands by Great Egrets at multiple scales in the southeastern USA. *Condor* 118: 46-56.
- Frederick, P., D. E. Gawlik, J. C. Ogden, M. I. Cook and M. Lusk. 2009. The White Ibis and the Wood Stork as indicators for restoration of the everglades ecosystem. *Ecological Indicators* 9S: S83-S95.
- Hancock, J. A., J. A. Kushlan and M. P. Kahl. 1992. Storks, ibises and spoonbills of the world. Academic Press, London, U.K.
- Herring, G., H. K. Herring and D. E. Gawlik. 2015. Social cues and environmental conditions influence foraging flight distances of breeding Wood Storks (*Mycteria americana*). *Waterbirds* 38: 30-39.
- Hexagon Geospatial. 2006. Erdas Imagine, v. 9.1. Hexagon Geospatial, Norcross, Georgia. <http://www.hexagongeospatial.com/products/producer-suite/erdas-imagine>, accessed 1 December 2015.
- Inskipp, C., H. S. Baral, S. Phuyal, T. R. Bhatt, M. Khatiwada, T. Inskipp, A. Khatiwada, S. Gurung, P. B. Singh, L. Murray and others. 2016. The status of Nepal's birds: the national red list series. Zoological Society of London, London, U.K.
- Kahl, M. P. 1971. Food and feeding behavior of Openbill Storks. *Journal für Ornithologie* 112: 21-35.
- Kalam, A. and A. J. Urfi. 2007. Foraging and prey size of the painted stork. *Journal of Zoology* 274: 198-204.

- Karki, S. and T. B. Thapa. 2013. Population status, nesting habitat selection and conservation threats of lesser adjutant stork (*Leptoptilos javanicus*) in the eastern lowlands of Nepal. *Conservation Science* 1: 27-35.
- Koju, R. 2015. Distribution, nesting tree preference, and nesting success of heronries in Rupandehi and Kapilbastu Districts, Nepal. M.S. Thesis, Khwopa College, Bhaktapur, Nepal.
- Lin, X. 1999. Inference in generalized additive mixed models by using smoothing splines. *Journal of the Royal Statistical Society* 61: 388-400.
- Maharjan, B. 2015. Food-provisioning behavior in heronries in Rupandehi and Kapilbastu Districts of Nepal. M.S. Thesis, Khwopa College, Bhaktapur, Nepal.
- Moritz, M., L. Maumary, D. Schmid, I. Steiner, L. Valloton, R. Spaar and O. Biber. 2001. Time budget, habitat use and breeding success of White Storks *Ciconia ciconia* under variable foraging conditions during the breeding season in Switzerland. *Ardea* 89: 457-470.
- Paudel, D., K. Adhikari, S. Baskota, S. Ranabhat, D. S. Pujara, S. Bhattarai, A. Shakaya, S. Gautam and P. Yadav. 2013. Environmental impact assessment of industrial development around Lumbini, the birthplace of Lord Buddha, World Heritage Property. IUCN Nepal, UNESCO Kathmandu, and Oriental Cultural Heritage Sites Protection Alliance, Nepal. <http://unesdoc.unesco.org/images/0021/002196/219616e.pdf>, accessed 1 December 2015.
- R Development Core Team. 2015. R: a language and environment for statistical computing, v. 3.2.3. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org/>, accessed 2 March 2016.
- Redondo, T., F. S. Tortosa and L. A. de Rayna. 1995. Nest switching and alloparental care in colonial white storks. *Animal Behavior* 49: 1097-1110.
- Sharma, S. 2006. Population status and distribution of Lesser Adjutant (*Leptoptilos javanicus*) in far-western lowland Nepal. *Tigerpaper* 33: 9-11.
- Sullivan, J. P. 1988. Effects of provisioning times and number fledged on nestling aggression in Great Blue Herons. *Colonial Waterbirds* 11: 220-226.
- Sundar, K. S. G. 2006. Flock size, density and habitat selection of four large waterbird species in an agricultural landscape in Uttar Pradesh, India: implications for management. *Waterbirds* 29: 365-374.
- Sundar, K. S. G. 2011. Agricultural intensification, rainfall patterns, and large waterbird breeding success in the extensively cultivated landscape of Uttar Pradesh, India. *Biological Conservation* 144: 3055-3063.
- Sundar, K. S. G. and S. Subramanya. 2010. Bird use of rice fields in the Indian subcontinent. *Waterbirds* 33 (Special Publication 1): 44-70.
- Sundar, K. S. G. and S. Kittur. 2012. Methodological, spatial and temporal factors affecting modeled occupancy of resident birds in the perennially cultivated landscape of Uttar Pradesh, India. *Landscape Ecology* 27: 59-71.
- Tourenq, C., R. E. Bennetts, H. Kowalski, E. Vialet, J. L. Lucchesi, Y. Kayser and P. Isenmann. 2001. Are rice fields a good alternative to natural marshes for waterbird communities in the Camarague, southern France? *Biological Conservation* 100: 335-343.
- Tourenq, C., S. Benhamou, N. Sadoul, A. Sandoz, F. Mesléard, J.-L. Martin and H. Hafner. 2004. Spatial relationships between tree-nesting heron colonies and rice fields in the Camarague, France. *Auk* 121: 192-202.
- U.S. Geological Survey. 2015. Landsat 8 data products. U.S. Department of the Interior, Geological Survey, Washington, D.C. <http://glovis.usgs.gov/>, accessed 10 November 2015.
- Wood, S. and F. Scheipl. 2014. gamm4: generalized additive mixed models using lme4 and mcgv. R package v. 0.2-3. <https://CRAN.R-project.org/package=gamm4>, accessed 2 March 2015.
- Zuur, A. F., E. N. Ieno, N. J. Walker, A. A. Saveliev and G. M. Smith. 2009. *Mixed effects models and extensions in ecology with R*. Springer, New York, New York.