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Roosting Ecology of Black-Headed Ibis (*Threskiornis melanocephalus*) in Urban and Rural Areas of Southern Rajasthan, India

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Abstract.—The roosting ecology of most waterbird species is poorly known and even less is known from southern Asia, where many species inhabit human-modified areas. Roosting ecology of the Black-headed Ibis (*Threskiornis melanocephalus*) was studied in urban and rural settings in southern Rajasthan, India. Analyses focused on assessing whether site characteristics varied between nest sites, urban and rural roost sites, and paired sites (i.e., a waterbird roost site near Black-headed Ibis roosts but without Black-headed Ibis). Additionally, the hypothesis that factors affecting Black-headed Ibis numbers at roosts would be similar at urban and rural sites was tested. Tree characteristics (canopy cover, girth at breast height) were different ($P < 0.05$) between nest and roost sites. Urban roost sites experienced 2.3 times greater disturbance than rural roost sites. Paired site characteristics were similar to urban roost sites (multi response permutation procedure, significance of $\delta = 0.3$), but were dissimilar to rural roost sites. Co-occurring roosting bird assemblages were significantly different between roosts and paired sites (significance of $\delta < 0.01$) in urban and rural settings. Black-headed Ibis numbers at urban roosts were influenced by multiple variables, but models showed considerable ambiguity at rural sites. Results strongly suggest that including roost sites in a species status assessment is important. *Received 21 July 2018, accepted 6 November 2018.*

Key words.—agricultural landscapes, Black-headed Ibis, co-occurring species, India, Rajasthan, roosting ecology, rural roosts, *Threskiornis melanocephalus*, urban roosts.

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Communal roosting is defined as an aggregation of unrelated conspecifics (more than two species or individuals) that spend diurnal or nocturnal resting time together. Individuals have the choice to use the same sites repeatedly alongside individuals of other species or conspecifics, or roost singly while not necessarily returning to the same place each time (Beauchamp 1999; Laughlin *et al.* 2014). It is a taxonomically widespread behavior occurring from lower invertebrates such as flatworms (e.g., *Cura foreman* and *Dugesia tigrina*) to mammals such as bats (e.g., *Myotis sodalis*), with aggregations numbering into the tens of thousands (Reynierse *et al.* 1969; Silvis *et al.* 2014). Communal roosting can improve fitness via reduced predation, increased thermoregulatory benefits, and foraging efficiency (Weatherhead 1983; Kramer 1985; Beauchamp 1999). Consequently, communal roosting sites can involve a considerable proportion of the species' population, making them an important facet of conservation measures (Donazar *et al.* 1996). The ecology of waterbird species are biased toward studies of foraging and breeding, while roosting behavior is poorly known for the majority of species. Roost sites can be different from breeding sites (Ogden 1990), suggesting that the absence of studies on this aspect constitutes a gap in understanding the ecology and conservation of waterbirds.

Characterizing roost sites can provide insights into habitat requirements for waterbirds during the non-breeding season. In natural settings, waterbird roost locations can be influenced by proximity to foraging habitats such as wetlands and grasslands (Pearson *et al.* 1992) and large, tall trees (Blanco 1996; Chevallier *et al.* 2010). However, when human activities dominate landscapes, presence of novel foraging sites such as rubbish dumps, well-watered gardens and swimming pools, and exotic tree species can be attractive for many bird species and eventually may alter roosting in natural habitats (Blanco 1996; Singh and Downs 2016). There is scarce

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information to assess whether the locations of roosting sites in exotic structures have similar characteristics to those found in natural structures (Bryan *et al.* 2002; Bowker and Downs 2012). Mixed species roosts have considerable advantages including improving feeding efficiency and reduced predation (Eiserer 1984). Composition of co-occurring roosting species can therefore be an important component of roosting behavior, but has not been well studied in waterbirds (Eiserer 1984). Another important but poorly understood aspect of waterbird roosting behavior is the size of flocks at roosts. In some waterbirds, roost sites with different flock sizes can share similar characteristics, especially in natural habitats (Bryan *et al.* 2002). Observational and experimental studies on non-waterbirds have suggested that flock size at roosts can be a function of resource distribution around roost sites (Ward and Zahavi 1973; Chapman *et al.* 1989), and represent individual roost site characteristics (Lambertucci 2013). Studies of waterbird roosting behavior have been conducted either in only natural or only urban settings, and it is not known if roosting ecology varies in different settings for the same species (Pearson *et al.* 1992; Chevallier *et al.* 2010; Singh and Downs 2016). Most studies on roosting ecology of waterbirds consider a small number of variables, and usually focus on a local scale (proximity to foraging habitats and roost tree characteristics).

Colonial waterbirds in southern Asia forage and breed in a variety of landscape and habitat conditions including natural wetlands, urban areas, and intensively cultivated rural landscapes (Sundar 2006; Koli *et al.* 2013; Sundar *et al.* 2016; Chaudhury and Koli 2018). Roosting behavior has been documented in several waterbirds species (Ali and Ripley 2007), but is very poorly understood for the near-threatened and colonial Black-headed Ibis (*Threskionis melanocephalus*; BirdLife International 2016). Black-headed Ibis use different habitats ranging from agricultural landscapes, densely-populated cities, and several kinds of natural and artificial wetlands (Balakrishnan and Thomas 2004; Sundar 2006; Chaudhury and Koli 2016; Chaudhary 2018) that represent a variety of conditions with differing levels of human disturbance and habitat availability. In this study, we describe Black-headed Ibis roosting ecology in southern Rajasthan, India, and evaluate whether roosting ecology varied between two disparate settings: urban and rural. No formal study of roosting ecology of a communal waterbird is available from southern Asia where human presence is ubiquitous and extensive.

Our objective was to document Black-headed Ibis roosting ecology focusing on site and tree characteristics, co-occurring roosting species, and factors affecting Black-headed Ibis flock sizes at roosts. We predicted that site and tree characteristics would vary between Black-headed Ibis roosting and nesting sites, between urban and rural Black-headed Ibis roost sites, and between roost sites and nearby "paired" sites that had waterbirds roosting without any Black-headed Ibis. We also predicted that assemblages of co-occurring roosting species would vary between roost and paired sites, but would be similar between Black-headed Ibis roosts located in urban and rural settings. Finally, we predicted that the same variables would affect Black-headed Ibis flock sizes at both urban and rural roosts.

METHODS

Study Area

The study was conducted in six districts of southern Rajasthan in northwestern India covering an area of 40,055 km^2 (Fig. 1). The region experiences strong seasonality with distinct winter (November-February), summer (March-June), and wet or monsoon (July-October) seasons. Total rainfall in the region averaged 867.8 mm. The highest temperature (~42 °C) was recorded in summer and lowest (~8 °C) in the winter season. The landscape was relatively heterogeneous and set within the old fold mountains of the Aravallis. Towns and cities in the focal districts had population densities (500-8,000 people/km^2; Office of the Registrar General and Census Commissioner, India 2011) magnitudes higher than rural areas and constituted urban settings marked by a dense concentration of buildings and related impervious surfaces. Only relatively large reservoirs, temple ponds and lakes were retained as urban wetlands. Most of these

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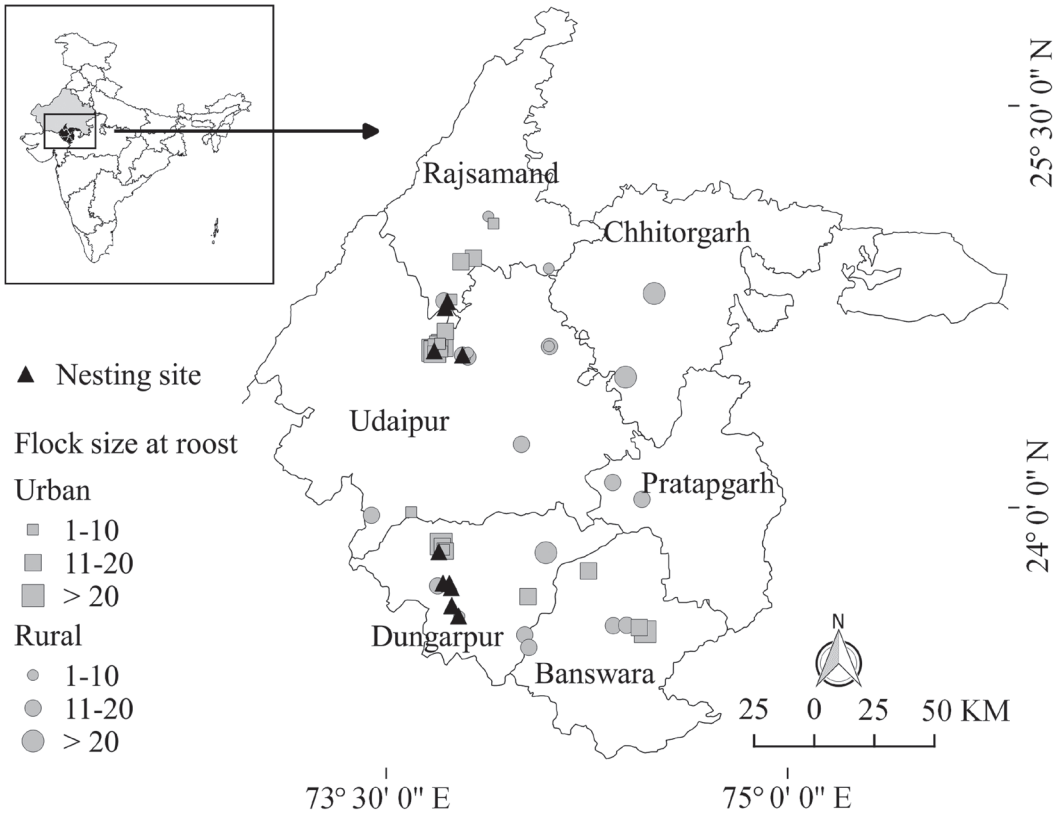


Figure 1. Locations and sizes of Black-headed Ibis nesting and roosting sites in urban and rural settings in southern Rajasthan, India. Inset shows location of Rajasthan state (gray) and focal districts (black) in India.

had boundary walls, and were heavily used for fishing and recreational boating (Koli *et al.* 2013). Agricultural areas alongside sparsely populated villages constituted the rural areas (population density varied between 190-400 people/km^2 at the district level; Office of the Registrar General and Census Commissioner, India 2011). Agriculture was the major rural land use supported by water from natural and artificial wetlands including reservoirs, marshes, village ponds, and lakes of various sizes (Choudhary 2018). Rural wetlands were used extensively year-round for grazing livestock, fishing and irrigation. Major crops were rice (*Oryza sativa*), maize (*Zea mays*), and soybean (*Glycine max*) during the monsoon, followed by wheat (*Triticum aestivum*) during the winter, and vegetables during the summer (Kulshreshtha *et al.* 2013). The region had few forested protected reserves, and outside these reserves, there were scattered trees both in the rural and urban areas. Trees outside reserves were exploited for timber, fruits, flowers, and leaves. A combination of utility-based attitudes, cultural norms, and formal protection ensured persistence of trees on the landscape. Urban and rural areas had sharp boundaries with no intermediate levels of variation in land use. Levels of urbanization varied between cities, and agricultural intensification varied between rural areas.

Locating Black-headed Ibis Nest, Roosts and Paired Sites

Black-headed Ibis roost sites were located by surveying along a road transect of a total of 2,561 km (356 km in Rajsamand; 563 km in Udaipur; 320 km in Dungarpur; 711 km in Banswara; 293 km in Pratapgarh; and 318 km in Chittorgarh) in June 2017 (see Chaudhury and Koli 2018). Nest sites were located during the breeding season in September 2017 when heronries were fully active (Chaudhury and Koli 2018). Roost and nest sites were located by direct observations and by following Black-headed Ibis flying to roosts or heronries. Presence of droppings below trees (roosts), nests on trees, and information given by local people helped identify potential nests and roosts. We visited each potential site to confirm nesting and roosting sites, and counted all Black-headed Ibis and other co-occurring roosting birds during visits. We identified a location as a roost site when two or more Black-headed Ibis assembled to spend the night, and a nest site when at least one active nest of the species was present. All roost and nesting sites were georeferenced using a hand-held Global Positioning System (Garmin eTrex 30x). At roosts,

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we counted Black-headed Ibis after birds stopped flying into the roost in the evening. We were interested in assessing whether Black-headed Ibis roost sites were distinct relative to roost sites that had other waterbirds, but no Black-headed Ibis. For these comparisons, we located paired roost sites without Black-headed Ibis using the same methods, but focusing on other species such as egrets, herons, other ibis species, and storks. Paired sites were located close to Black-headed Ibis urban and rural roost sites.

Variables

At each nest, roost and paired site, we measured variables corresponding to three broad aspects of roosting ecology. The first related to proximity to potential foraging habitat and human disturbance. We measured the distance (m) from each site to the nearest wetland, stream or river. We measured proximity to human disturbance as the distance (m) to the nearest road and human habitation. We used Google Earth Pro (2018) for all measurements. The second aspect related to tree and site characteristics at sites. We made a number of measurements to characterize the tree and the human disturbance level at each site. We measured tree height (m) using a clinometer (Brunton Omni-slope), and girth at breast height (m) using a regular measuring tape. We estimated canopy cover (m^2) by measuring the longest and widest edges of canopies, averaging and halving the measures, and using the radius value to estimate the area of a circle. We counted the number of available trees within a 100 x 100-m area around nest, roost and paired sites. We computed an index of human disturbance at sites. We allocated a score for three different types of disturbance recorded within 30 m of the site between 07:30 and 09:00 hr (peak activity times; see Rao and Koli 2017) as follows: number of pedestrians (1: 1-30, 2: 31-60, 3: 61-90, 4: 91-120, 5: > 120); number of vehicles passing (1: 1-90, 2: 91-180, 3: 181-270, 4: 271-360, 5: > 360); and number of parked vehicles (1: 0-3, 2: 4-6, 3: 7-9, 4: 10-12, 5: > 12). The disturbance index was computed by summing scores across all three types of measured disturbance (Soh *et al.* 2002). Finally, we listed and counted all co-occurring roosting species at roost and paired sites.

Statistical Analysis

Comparing tree and site characteristics between nesting, roosting and paired sites. We carried out exploratory analyses to determine if variables differed between sampled sites. We carried out *t*-tests in statistical program SPSS (SPSS Inc. 2011) to identify individual variables that differed between sites across a range of paired comparisons. We used two-sample *t*-tests when comparisons had unequal sample sizes (e.g., nest sites vs. urban roost sites), and paired *t*-tests when sample sizes were equal (e.g., urban roost sites vs. paired sites). We used the multi-response permutation procedure (MRPP) to test the hypothesis of no difference in measurements of variables between sites. MRPP is a non-parametric multivariate procedure that does not require assumptions of multivariate normality and homogeneity of variance of the data (Cai 2006). We present both the effect size "A" (chance-corrected within-group agreement), and a significance test, "δ", that is the outcome of 1,000 permutations. We used the package 'vegan' in statistical program R (Oksanen *et al.* 2018), specifying Bray-Curtis distance to compute dissimilarity matrices, for MRPP analyses.

Associations with co-occurring roosting birds. The abundance of birds was used to evaluate whether individual species and the full complement of co-occurring species differed between paired and Black-headed Ibis roost sites, and between Black-headed Ibis urban and rural roost sites. We computed the "simple index of association", which is the probability that two individuals are observed together given that one of them has been seen, following Ginsberg and Young (1992). The simple index is free of biases of sample size, double counts and potential overestimations (Ginsberg and Young 1992; Hoppitt and Farine 2018). The index ranges from 0-1, with higher values indicating species found more often or associated more with the target species. We segregated species into three broad feeding guilds (carnivore, omnivore, piscivore) and two species from additional guilds (Asian Openbill *Anastomus oscitans*, obligate snail eater; Rose-ringed Parakeet *Psittacula krameri*, frugivore) and graphically assessed if associations with Black-headed Ibis varied across foraging guilds. We tested the hypothesis that waterbird assemblages at roosts would favor omnivores in two ways. First, we hypothesized that assemblages would vary between Black-headed Ibis roost sites and paired sites, but would be similar at urban and rural roost sites. We used abundance matrices of co-occurring species and conducted MRPP to test hypotheses. Secondly, we compared the number of species in each feeding guild between roosting and paired sites testing the null of no difference in guild-wise species richness using a χ^2-test of independence. The χ^2-test was carried out manually using Microsoft Excel.

Factors affecting Black-headed Ibis flock sizes at roosts. We assessed collinearity among variables by undertaking bivariate correlations separately for urban and rural roost sites, and retained only weakly correlated variables (Pearson's correlations, $P > 0.05$). For both urban and rural roost sites, these included number of co-occurring roosting species (CS), distance to wetland (DTW), tree height (TH), and number of available trees (ATS). We used generalized additive models (GAM) to relate variables with observed Black-headed Ibis flock sizes at roosts. GAM is a non-parametric extension of the more commonly used generalized linear models, and useful to fit models with over-dispersed data sets with non-linear relationships. We ran the full complement of single-variable models, the null model and the full model with all four variables. We also ran two additional models (CS+DTW and CS+TH+ATS) that we decided on *a priori*, for each setting. We used the multimodel information-theoretic inference framework and computed Akaike Information Criteria (AIC) to compare among competing models using package 'gam' in statis-

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tical package R (Hastie 2013). We used a difference of two AIC units between competing models to signify they were different (Burnham and Anderson 2002).

RESULTS

Fifty Black-headed Ibis roosting sites (24 in urban and 26 in rural settings) and 13 nesting sites were located (Fig. 1). Cumulative Black-headed Ibis numbers were much higher at roost sites (n = 336 and 328 in urban and rural roost sites, respectively) compared to nesting sites (n = 207). Black-headed Ibis numbers were highest at nesting sites (average = 15.9 ± 8.7 SD; Range = 3-50), with fewer birds at each urban (average = 14.0 ± 8.7 SD; Range = 1-33) and rural (average =12.6 ± 7.0 SD; Range = 3-35) roost site.

Comparing Nest, Roost and Paired Site Characteristics

Black-headed Ibis nest (n = 13) and roost (n = 50) sites had similar measures for proximity to potential foraging habitat and human habitation ($P > 0.05$; Table 1). The disturbance index was similar between nest and urban roost sites (two-sample t-test; t = 0.20; P = 0.84), but was significantly different between urban and rural roost sites (two-sample t-test; t = -6.21; $P < 0.01$), with urban roost sites experiencing 2.3 times higher disturbance (Table 1). Except for the number of available trees, all other tree characteristics varied significantly ($P < 0.05$) between nest and roost sites, with nest sites having the lowest values (Table 1). Tree height, canopy cover and girth measurements were significantly higher ($P < 0.05$) at urban roost sites compared to rural roost sites.

Nest site characteristics varied significantly between both urban and rural roost sites (MRPP; A = 0.07; significance of $\delta < 0.01$). Characteristics of urban roost sites also differed significantly from rural roost sites (A = 0.02; significance of $\delta < 0.04$). Characteristics of roost sites were similar to paired sites in urban settings (A = 0.003; significance of $\delta = 0.3$). Rural roost sites, however, were dissimilar from paired roost sites at the 94% significance level (A = 0.02; significance of $\delta = 0.06$).

Associations With Co-occurring Roosting Species

The simple index of association computed for 16 species at Black-headed Ibis roost sites showed eight species were associated more with Black-headed Ibis (simple index > 0.2) at both urban and rural roost sites (Fig. 2). Simple index values for individual species varied similarly across urban and rural roost sites (Pearson's r = 0.88; $P < 0.01$). Black-headed Ibis were associated more with Lesser Cormorant (*Microcarbo niger*), Great Egret (*Ardea alba*) and Cattle Egret (*Bubulcus ibis*) and to a lesser degree with Oriental Darter (*Anhinga melanogaster*), Intermediate Egret (*A. intermedia*), Eurasian Spoonbill (*Platalea leucorodia*), Asian Openbill, and Black-necked Stork (*Ephippiorhynchus asiaticus*; Fig. 2). Painted Storks (*Mycteria leucocephala*) had five times higher index value in rural roost sites relative to urban roost sites. Urban and rural sites had similar assemblages of co-occurring roosting species (MRPP; A = -0.003; significance of $\delta = 0.63$). However, assemblages at Black-headed Ibis roosts differed significantly from assemblages at paired sites at both urban (A = 0.08; significance of $\delta < 0.01$) and rural (A = 0.08; significance of $\delta < 0.01$) settings. Species richness across guilds varied between roost and paired sites with carnivore species dominating at all sites (Fig. 3), but this difference was not statistically significant ($\chi^2_9 = 2.29$; $P > 0.1$).

Factors Affecting Black-headed Ibis Flock Size at Urban and Rural Roosts

Model comparisons for Black-headed Ibis urban roosts showed the full model to be the best model, being 3.3 AIC units lower than the subsequent competing model (Table 2). All the next three best models included number of co-occurring species, were within 2 AIC units of each other, and had more support than the null model by > 10 AIC units. In contrast, models showed consider-

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Table 1. Summary statistics of variables measured at Black-headed Ibis nest and roost sites, and paired sites (without Black-headed Ibis) in southern Rajasthan, India. Settings with significantly different measures for a particular variable are indicated with the same superscripted letter (*t*-tests, $P < 0.05$). Distance to road, human habitation, and wetland, and disturbance index are variables measuring proximity to potential foraging sites and human presence. Numbers are mean ± SD (Range).

		Urban Sites		Rural Sites	
Variable	Nest Sites ($n = 13$)	Roost ($n = 24$)	Paired ($n = 24$)	Roost ($n = 26$)	Paired ($n = 26$)
Distance to road	62.88 ± 135.50 (0.50-500.00)	33.30 ± 60.37 (0.50-250.00)	85.33 ± 178.80 (0.00-700.00)	143.60 ± 287.20 (1.00-1100.00)	109.00 ± 207.00 (0.00-700.00)
Distance to human habitation	43.31 ± 57.97 (1.00-200.00)	38.95 ± 64.17 (1.00-255.00)	53.21 ± 158.30 (0.00-750.00)	90.12 ± 131.3 (1.00-578.00)	48.38 ± 96.64 (3.00-500.00)
Distance to wetland	125.50 ± 413.30 (0.00-1500)	140.00 ± 231.40 (0.00-800)	148.50 ± 213.30 (0.00-800.00)	36.90 ± 98.84 (0.00-502.00)	51.81 ± 84.00 (0.00-300.00)
Disturbance index	8.38 ± 6.34 (0.00-16.00)[a]	8.00 ± 3.48 (3.00-14.00)[b]	8.29 ± 3.95 (1.00-14.00)	3.42 ± 0.94 (3.00-7.00)[abc]	5.03 ± 3.14 (1.00-13.00)[c]
Tree height	10.58 ± 3.26 (5.00-15.00)[a]	18.58 ± 7.44 (7.00-32.00)[ab]	26.44 ± 13.29 (10.00-50.6)[b]	14.73 ± 5.31 (8.70-29.40)[ac]	30.36 ± 14.04 (11.30-57.10)[c]
Canopy cover	84.69 ± 42.46 (26.40-200.20)[a]	190.30 ± 63.99 (0.00-287.30)[a]	183.50 ± 51.48 (25.80-287.40)	180.40 ± 46.93 (92.50-267.30)[ab]	216.60 ± 46.50 (136.10-296.70)[b]
Girth at breast height	0.55 ± 0.29 (0.15-1.00)[a]	1.74 ± 1.00 (0.00-4.20)[a]	5.80 ± 19.23 (0.78-96.00)	1.51 ± 0.80 (0.62-3.00)[ab]	2.21 ± 1.13 (0.55-4.70)[b]
Number of trees around site	2.46 ± 1.61 (0.00-5.00)	3.62 ± 2.10 (1.00-9.00)	4.37 ± 1.76 (1.00-8.00)	2.92 ± 1.57 (1.00-6.00)	3.15 ± 1.48 (1.00-7.00)
Number of co-occurring roosting species	4.07 ± 1.70 (1.00-8.00)	3.66 ± 2.82 (0.00-10)[a]	1.83 ± 0.96 (1.00-4.00)[a]	3.80 ± 2.31 (0.00-8.00)	2.73 ± 1.68 (1.00-6.00)
Abundance of co-occurring roosting species	49.15 ± 44.24 (8.00-177.00)	52.54 ± 62.38 (0.00-250.00)[a]	18.67 ± 9.78 (5.00-38.00)[a]	46.73 ± 50.6 (0.00-180.00)[b]	22.31 ± 12.77 (4.00-53.00)[b]

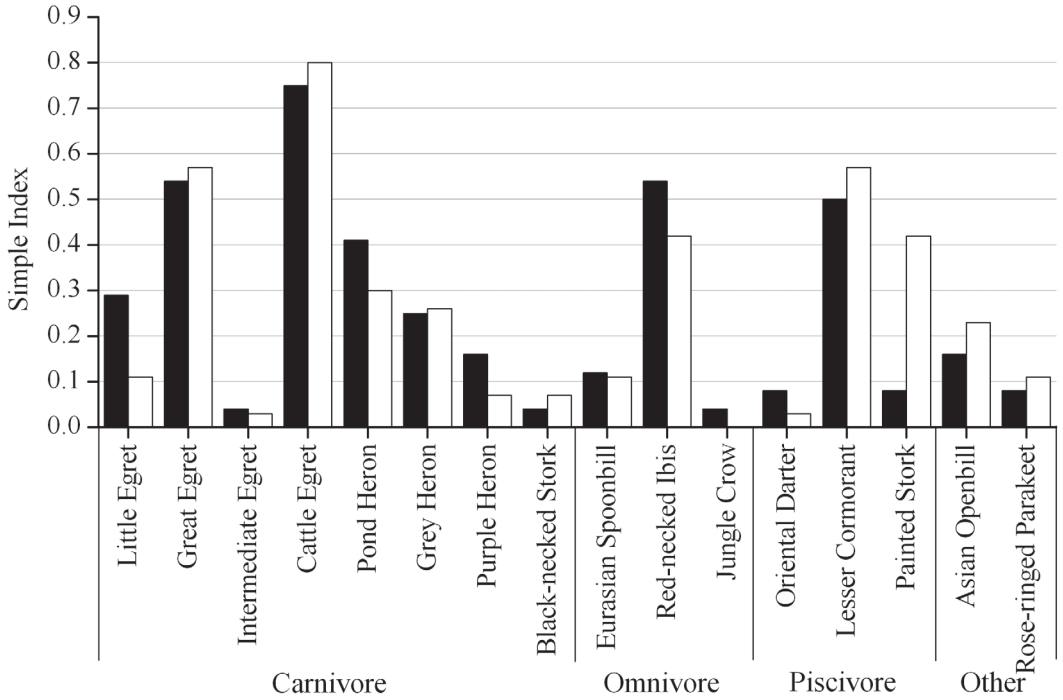


Figure 2. Simple index values showing associations of species with Black-necked Ibis at urban (black) and rural (white) roost sites. Co-occurring species are categorized into feeding guilds.

able uncertainty in rural settings with the null model being the model with the most support (lowest AIC at 178.4; Table 3), and subsequent competing models were within 2 AIC units of each other.

DISCUSSION

Our results showed that urban and rural settings were equally important as roost sites for Black-headed Ibis, and that Black-headed Ibis numbers at roost sites were three times higher than at nest sites. In addition, roost site characteristics were different from nest sites suggesting that conservation planning for the species should also take into account preservation of roost sites. Black-headed Ibis still maintained roost sites in high disturbance urban sites. Our results agree with a study on heronry locations across India that also found a high human tolerance for heronries located in urban settings (Subramanya 1996). Absence of differences in proximity to potential foraging sites across urban and rural settings suggests adequacy of foraging sites in southern Rajasthan. Conversely, it also suggests that Black-headed Ibis likely forage in habitats that are not just assumed potential foraging sites such as wetlands or rivers. This finding matches observations in southern Rajasthan (Chaudhury and Koli 2018) and Uttar Pradesh (Sundar 2006) where Black-headed Ibis foraged in a variety of habitats throughout the year. Trees were much larger at roost sites relative to nest sites, particularly in urban settings. Roost and paired sites were different only in rural settings suggesting that conditions in rural landscapes for roosting waterbirds are more diverse.

Similarity in associations of roosting Black-headed Ibis with co-occurring species in urban and rural settings is a novel finding, and matched our expectations. In part, this suggests that urban and rural settings are equally hospitable for the observed 16 co-occurring species. The list includes globally near-threatened species such as Oriental Darter, Eurasian Spoonbill, Painted Stork

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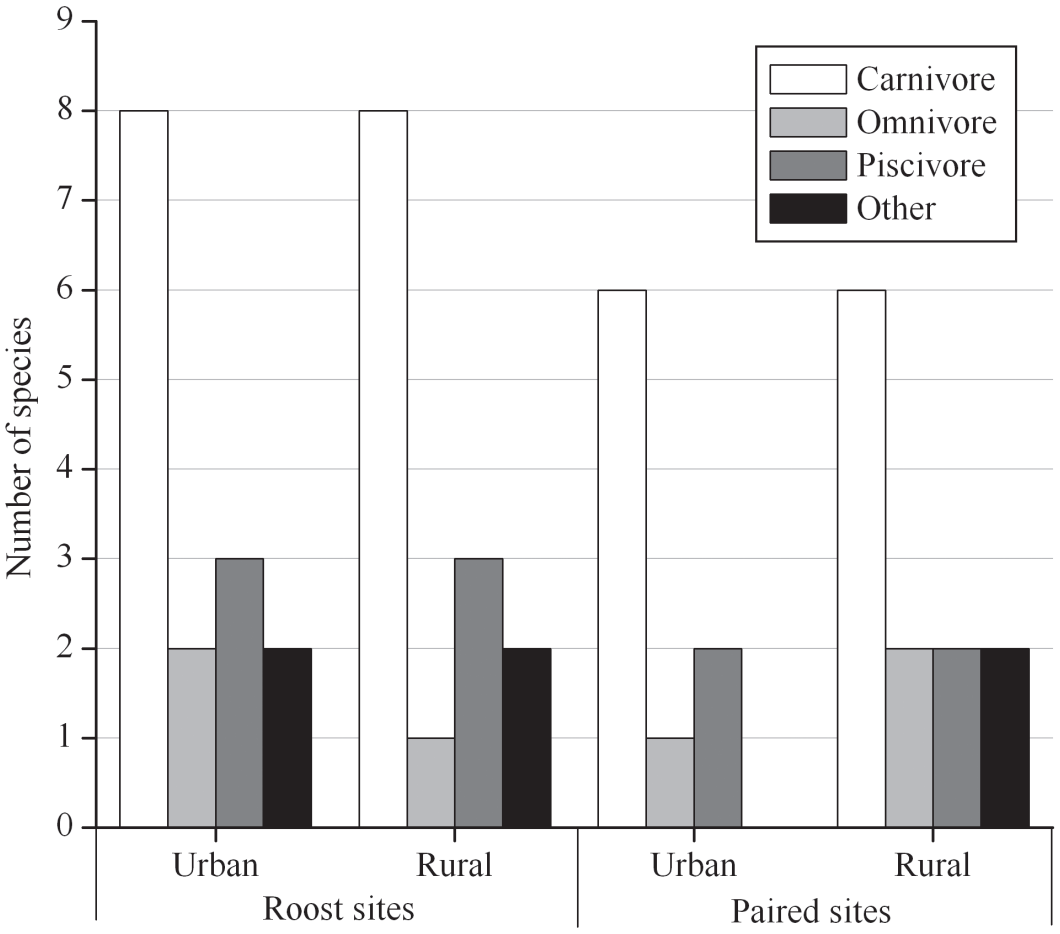


Figure 3. Species richness across feeding guilds of co-occurring bird assemblages at Black-headed Ibis roost sites and at paired sites.

and Black-necked Stork (Fig. 2). Assemblages of co-occurring species varied between Black-headed Ibis roost and paired sites suggesting that these assemblages are non-random.

A combination of variables influenced flock sizes at Black-headed Ibis urban roosts. However, contrary to our prediction, measured variables were inadequate to explain flock sizes at rural roosts. Black-headed Ibis flock sizes increased at roosts as numbers of co-occurring species increased, further suggesting mutual benefits for all the species. Poor support for distance to wetlands alone influencing flock sizes is not easily explainable. However, results suggest that, in addition to foraging habitat, associating with other species is a key component of Black-headed Ibis roosting ecology in southern Rajasthan.

Our findings provide an understanding of roosting ecology for a large waterbird in southern Asia. The observed importance of co-occurring species at Black-headed Ibis roosts would seem to suggest that a behavioral study in southern Asia would yield novel insights. This study also supports the conservation value of roost sites, even in relatively busy urban settings, to Black-headed Ibis. Status assessments currently identify deterioration of foraging wetland habitat and disturbance at nesting colonies as important aspects of conservation of Black-headed Ibis (BirdLife International 2016). Assessments should include the identification and maintenance of roosting sites as an important

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Table 2. Model selection statistics for factors affecting Black-headed Ibis flock sizes at roosts in urban settings in southern Rajasthan, India. Variables are: CS – number of co-occurring roosting species; DTW – distance to the nearest wetland; TH – tree height; and ATS – number of trees around roost trees. The full model includes all four variables.

Model	AIC	ΔAIC	Deviance
Full	157.65	0.00	223
CS + DTW	160.95	3.30	499
CS + TH + ATS	162.86	5.21	387
CS	164.40	6.74	804
Null	175.16	17.51	1,758
DTW	177.10	19.45	1,366
TH	177.39	19.74	1,382
ATS	178.77	21.12	1,464

conservation strategy. While previous studies (Sundar and Kittur 2012, 2013; Sundar *et al.* 2015, 2016) have discovered the high value of agricultural landscapes in southern Asia to waterbirds, the discovery of crowded urban settings supporting high populations of waterbird species outside of the breeding season is novel. This bodes well for species conservation in the region, and provides an optimistic overtone to Black-headed Ibis status assessments.

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Table 3. Model selection statistics for factors affecting Black-headed Ibis flock sizes at roosts in rural settings in southern Rajasthan, India. Variables are: CS – number of co-occurring roosting species; DTW – distance to the nearest wetland; TH – tree height; and ATS – number of trees around roost trees. The full model includes all four variables.

Model	AIC	ΔAIC	Deviance
Null	178.40	0.00	1,246
CS	180.00	1.56	973
TH	182.00	3.60	1,052
DTW	183.00	4.32	1,081
CS + TH + ATS	183.20	4.79	595
CS + DTW	185.00	6.57	867
ATS	186.30	7.87	1,240
Full	188.80	10.37	542

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