

# Is the Red-naped Ibis *Pseudibis papillosa* a “waterbird”? Distribution, abundance and habitat use in landscapes with two different dominant land uses in Udaipur district, Rajasthan, India

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**Abstract** Wetland and agricultural landscapes provide prime habitats for a variety of waterbirds. In tropical and sub-tropical areas, such landscapes experience considerable variation due to seasonal changes in water availability and crops. We asked how the Red-naped Ibis *Pseudibis papillosa*, an endemic and poorly studied waterbird that is assumed to not be closely tied to wetlands, coped with seasonal changes in a semi-arid region of India. We hypothesized that ibises respond differently to seasonal changes when the dominant land use varied (wetlands versus agriculture). We documented Red-naped Ibis abundance (as encounter rate), flocking and habitat use across three seasons in Udaipur district, Rajasthan, India. We used an *a-priori* field design that allowed coverage of focal areas that were dominant in either wetlands or agriculture. In all three seasons, wetland-dominated areas had magnitudes more ibises relative to agriculture-dominated areas. Ibises showed strong seasonal variation in encounter rates, flock size, and habitat use in both landscapes. Red-naped Ibis preferred wetland habitats throughout the year, though a majority were sighted in fallow fields with none using fields with standing crop in either landscape. Our findings suggest that Red-naped Ibis are closely associated with wetlands and that seasonal variations in landscape conditions, especially occurrence of fallow fields, cause ibises to change some of their habits. Existing literature on the species' habits require being updated. Similar careful studies conducted in a variety of conditions are essential to understand if coping mechanisms of Red-naped Ibis vary with crop type and local climate.

**Keywords** Agricultural and wetland landscapes, encounter rate, habitat selection, north-west India, Rajasthan.

## Introduction

Agricultural fields are studied globally to understand waterbird ecology and distribution with the vast majority of studies based in developed countries. Agrarian lands have been viewed as a primary waterbird habitat under certain conditions, especially low human presence (Czech and Parsons 2002; Pierluissi 2010).

However, studies of waterbirds in agricultural areas in both temperate and tropical countries have reported substantial populations of waterbirds such as herons, cranes, and storks reliant on human-dominated landscapes, notwithstanding natural wetlands being greatly reduced by a burgeoning human population and expanding cultivation (Kushlan and Hafner 2000; Sundar and Subramanya 2010; Sundar 2011; Kittur and Sundar 2020; Kittur and Sundar 2021). In tropical areas with rice as the principal crop, the landscape experiences significant seasonal changes in conditions related to water availability and primary

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crop cultivated. How waterbirds use such crop fields and how resident species cope with these seasonal changes is being increasingly documented (González-Solis *et al.* 1996; Marques and Vicente 1999). In countries such as India where rice is a dominant crop, there are substantial areas that are arid and rocky with rice cultivation restricted to a few patches, such as in southern Rajasthan (Koli *et al.* 2019). While several waterbirds have been documented using such landscapes, there is limited understanding of how resident waterbirds fare in such landscapes without rice and with seasonal variations in conditions.

An increasing number of studies in South Asia have showcased the high value of agricultural landscapes that retain a mosaic of crop fields and wetlands for waterbird populations, including several globally threatened species (Sundar 2006; Sundar and Kittur 2013; Sundar *et al.* 2015; Frank *et al.* 2021, Kittur and Sundar 2021; Ghimire *et al.* 2022). Community-managed wetlands maintained within agricultural landscapes primarily for human and livestock use, and to water crops, also support considerable bird diversity despite heavy human use and complicated hydrology (Sundar *et al.* 2015; Sundar and Kittur 2013). Waterbirds responses to season and location, however, varies depending on the landscape, cropping pattern and the species.

In a rice-dominated landscape, the flock sizes of territorial Black-necked Stork *Ephippiorhynchus asiaticus* did not vary across seasons or habitats, and storks used both natural (wetlands) and artificial (agriculture fields, irrigation canals) habitats to a varying degree (Sundar 2004). Contrary to the above pattern, flock sizes and densities of gregarious species such as the Black-headed Ibis *Threskiornis melanocephalus*, Painted Stork *Mycteria leucocephala* and Woolly-necked Stork *Ciconia episcopus* were significantly higher after nesting likely due to immature fledged birds' aggregating with adults (Sundar 2006). The extent of available wetlands affected Asian Openbill *Anastomus oscitans* flock size and habitat use across seasons possibly due to its specific food habits (freshwater snails) and the varied availability of this food in fields and wetlands seasonally (Sundar 2006). In a multi-scale, multi-

year study across several landscapes where rice was the dominant crop in one season, Woolly-necked Storks showed considerable complexity in densities and habitat use with both metrics varying seasonally and across locations (Kittur and Sundar 2020). The majority of the storks used agricultural fields (in proportion to their availability) while preferring (used more relative to availability) wetlands in most landscapes (Kittur and Sundar 2020). In a two-year landscape-scale survey across southern Rajasthan where rice is rare, Black-headed Ibis, a flocking species, was observed using multiple habitats but did not vary habitat use seasonally (Chaudhury and Koli 2018). Black headed Ibises predominantly used wetlands while occasionally using other habitats such as crop fields, sewage lines and garbage disposal sites (Chaudhury and Koli 2018). In yet another study in the rice-dominant landscape of Gujarat, India, Glossy Ibises *Plegadis falcinellus* showed strong scale dependant habitat use with preference for areas with intermediate levels of wetlands (50-100 ha of wetlands in grids of size 10 × 10 km) but changed preference to areas with the most wetlands during the dry summer season (Sundar and Kittur 2019). In another Indian state, Haryana, a district where the majority of wetlands have been illegally converted to fishponds, reduction of water levels caused by irrigation for surrounding crop fields improved the use of such wetlands by few waterbirds (Sundar *et al.* 2015). These studies collectively show that while agricultural landscapes provide excellent habitats for waterbirds overall, the variation in habitat use and population densities with seasons is species-specific.

One large waterbird species that is widely distributed across the Indian subcontinent is the poorly studied Red-naped Ibis *Pseudibis papillosa* (Ali and Ripley 2007). Available observations suggest that it is a species less dependent on wetlands relative to other sympatric ibis species and is thought to be a habitat generalist. It has been observed foraging in a wide range of habitats such as drier margins of wetlands, grasslands, paddy fields, fallow crop fields, open sewage channels, garbage dump sites, and sand dunes (Ali and Ripley 2007; Soni 2008; Hancock *et al.* 2011). Systematically collected empirical information on the species is rare and biased towards agricultural



landscapes dominated by rice in at least one season. Two such studies found that Red-naped Ibises use these landscapes in small numbers (Sundar and Kittur 2013; Katuwal and Quan 2022). Red-naped Ibises in lowland Nepal mostly nest on trees in forested areas seemingly avoiding agricultural areas for breeding (Katuwal and Quan 2022). Red-naped Ibises were common, widespread residents in one city in Rajasthan, India – Churu – but showed strong seasonal changes in abundance, used different foraging sites and preferred nesting on trees within the city (Soni 2008).

There is no systematically collected empirical information on how Red-naped Ibises cope with seasonal changes in relatively arid agricultural landscapes where rice is not the dominating crop. We designed a study across Udaipur district to understand the habits of this species, particularly abundance, flocking habits, and habitat use across a full year. Udaipur was ideal for this study since rice is rare as a crop across the district. The region is semi-arid, and much rockier relative to the areas where majority of waterbird studies have been carried out globally (Koli *et al.* 2019). In settings such as these, where wetlands and agriculture are sparser on the landscape relative to areas cultivated with rice, and where seasonal variations are much starker, we asked how Red-naped Ibises would respond to seasonal changes? Given existing assumptions regarding Red-naped Ibises not being a wetland bird (Hancock *et al.* 2011), would responses be similar in areas where wetlands were more common relative to areas dominant with agriculture? We hypothesized that Red-naped Ibises would: (1) use wetland-dominated and agriculture-dominated landscapes differently with variations apparent in metrics such as abundance and flock sizes; (2) show less seasonal variation of population metrics in wetland-dominated landscapes relative to agriculture-dominated landscapes; and (3) not show a strong preference for wetlands as foraging habitat, notwithstanding whether the landscape was dominated by wetlands or agriculture. Landscape scale studies with an *a-priori* design stratifying a landscape based on dominant land uses relevant to waterbird ecology are rare and have previously been developed across the Gangetic flood plains where areas with different

amounts of rice grown were identified and sampled (Sundar and Kittur 2013). This study is the first where the *a-priori* stratification includes two major land uses – wetlands and agriculture.

## Study area

Udaipur district (~13,419 km<sup>2</sup>) is located in the southern part of the state of Rajasthan, India (Figure 1a). The Aravalli Mountain range dominates the western and south-western parts of the district providing rocky relief to the geography leading to considerably low water availability relative to the wetter, flatter northern and eastern parts of the district (personal observations). The north-eastern parts of the district have extensive fertile plains that are utilized for agriculture (Figure 1c). Both artificial and natural wetlands are interspersed across the district providing potentially high-quality habitat for wetland dependent fauna (Chaudhury and Koli 2018; Koli *et al.* 2019). Specific studies documenting the kinds of wetlands and how they are managed are not available for the region. The human population of the district is 26.33 million, out of which ~55 % are tribal who primarily depend on agriculture and animal husbandry for their livelihood (Census India 2011).

The district experiences three distinct seasons namely monsoon (or rainy season; July - October), winter (November-February) and summer (March - June) that are differentiated by distinct temperature and precipitation profiles. Average annual rainfall is ~772 mm and temperature ranges from 1° - 25° C in winter to 26° - 48° C in summer (averaged for 2016 - 2020; data from Water Resources, Government of Rajasthan 2016-2020). Cropping is also distinctly seasonal with each growing season having local names such as Kharif (June - September), Rabi (October - February), and Zayad (March - June; Jat *et al.* 2004). The primary Kharif crops include Maize *Zea mays*, Jowar *Sorghum bicolor*, and Urad dal *Vigna mungoi*, whereas the Rabi crops are Wheat *Triticum aestivum*, Barley *Hordeum vulgare*, and Mustard *Brassica juncea*. During the summer, the primary Zayad cultivated crops are Watermelon *Citrullus lanatus*, multiple vegetables, and fodder crops such as Alfalfa *Medicago sativa*, Berseem Grass *Trifolium alexandrinum*, and Great Millet *Sorghum bicolor*. Natural wetlands fill during the monsoon and are used to water crops in the other seasons, though the majority of them dry up at the end of winter resulting in a rapid and significant reduction of wetlands during summer. The larger reservoirs have some water throughout the year and are used for various purposes including fish rearing (personal observations).

## Methods

### Field design

We developed a land use map of Udaipur district using



satellite imagery that was used to identify the two focal strata – areas dominating in wetlands or agriculture. Three western tehsils of the district, namely Gogunda, Kotra and Jhadol, were entirely hilly and inaccessible, and were excluded from our study (Figure 1b). Four Sentinel-2 (Level-2A; <https://scihub.copernicus.eu>) images of 10 x 10 m resolution with the least cloud cover (two images dated 19 December 2019 and two dated 29 December 2019) were downloaded and clipped using the shape file of study area (shaded part of Figure 1b). All images were classified separately into four broad land classes, namely agriculture (agriculture fields with crops), built-up (included buildings and roads), water (included seasonal and permanent lakes, ponds, and rivers), and other (a mix of various other land uses that had considerable overlaps in spectral signature including tree patches, scrubland and open areas that included fallow fields) using the ‘Maximum likelihood’ algorithm in Semi-automatic Classification Plugin (SCP; Congedo 2021) in QGIS freeware (ver. 3.10 ‘A Coruña’; QGIS Development Team 2019). Some misclassified regions were identified and corrected manually by using Google map as a references layer. For this, the Serval Plugin (<https://www.lutraconsulting.co.uk/blog/2016/09/05/serval/>) and Edit Raster tool in the post processing menu of SCP were used. The classified and cleaned images were then mosaicked to form a single raster image. The overall accuracy of the classified imagery was 90 % (Kappa = 0.86).

The focal study area was overlaid with a grid of hexagonal units (shape chosen to reduce edge effects) with each side measuring 1.96 km providing an area of

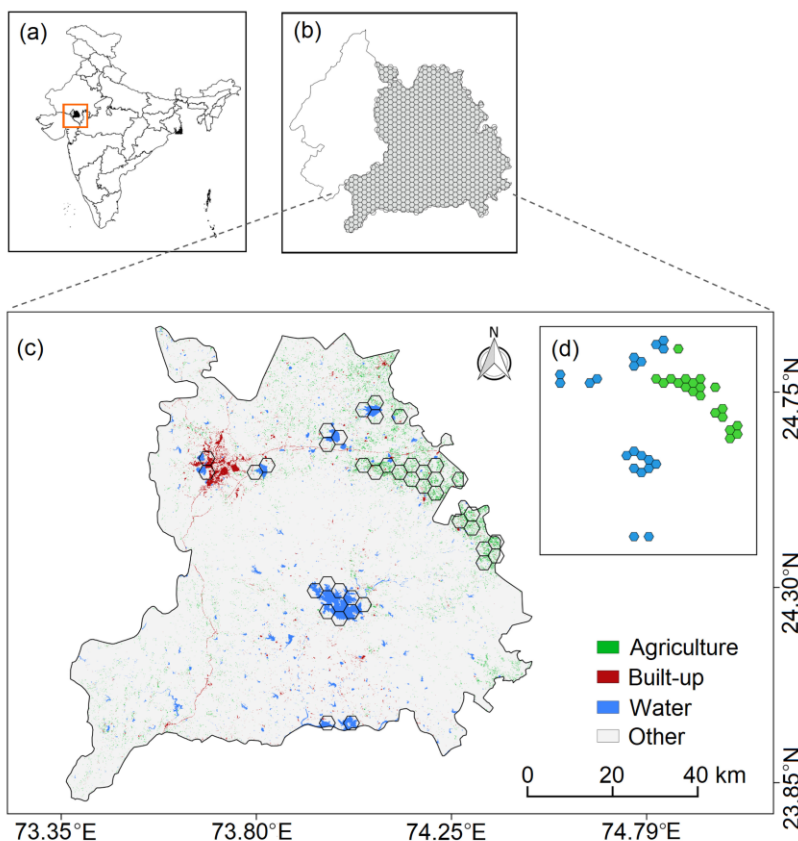
10 km<sup>2</sup> per hexagon. We calculated the area of each land class category in each hexagon and selected 20 grids having the most wetland area (range 1.64 - 8.71 km<sup>2</sup>/ hexagon) as “wetland hexagons” and 20 hexagons with the most agriculture area (range 1.25 - 2.50 km<sup>2</sup>/ hexagon) as “agriculture hexagons” for field surveys (Figure 1c, d).

#### Field surveys

We surveyed focal hexagons from 1 July 2021 to 30 May 2022 covering each hexagon once every season on days without rain and fog. Surveys started at sunrise and ended before 1100 h. For surveying hexagons, we used the network of metalled roads which ensured that coverage remained nearly the same in all three seasons. All available motorable roads in each hexagon were traversed. We searched for Red-naped Ibises, driving on a motorbike at *c.* 20 km/ hr. and a hand-held GPS was used to record tracks (to calculate transect length in km) and bird locations. All individuals of Red-naped Ibises visible within *c.* 300 m on either side of the road were counted. At large wetlands, we used vantage points to scan for ibises with 10 × 50 binoculars. Whenever ibises were sighted, we noted the following: location of sighting (latitude - longitude), number of individuals, number of adults and younger birds (identified by duller red coloration on the head; see Figure 2), and broad habitat category that ibis were using (agriculture, built-up, wetland, and others).

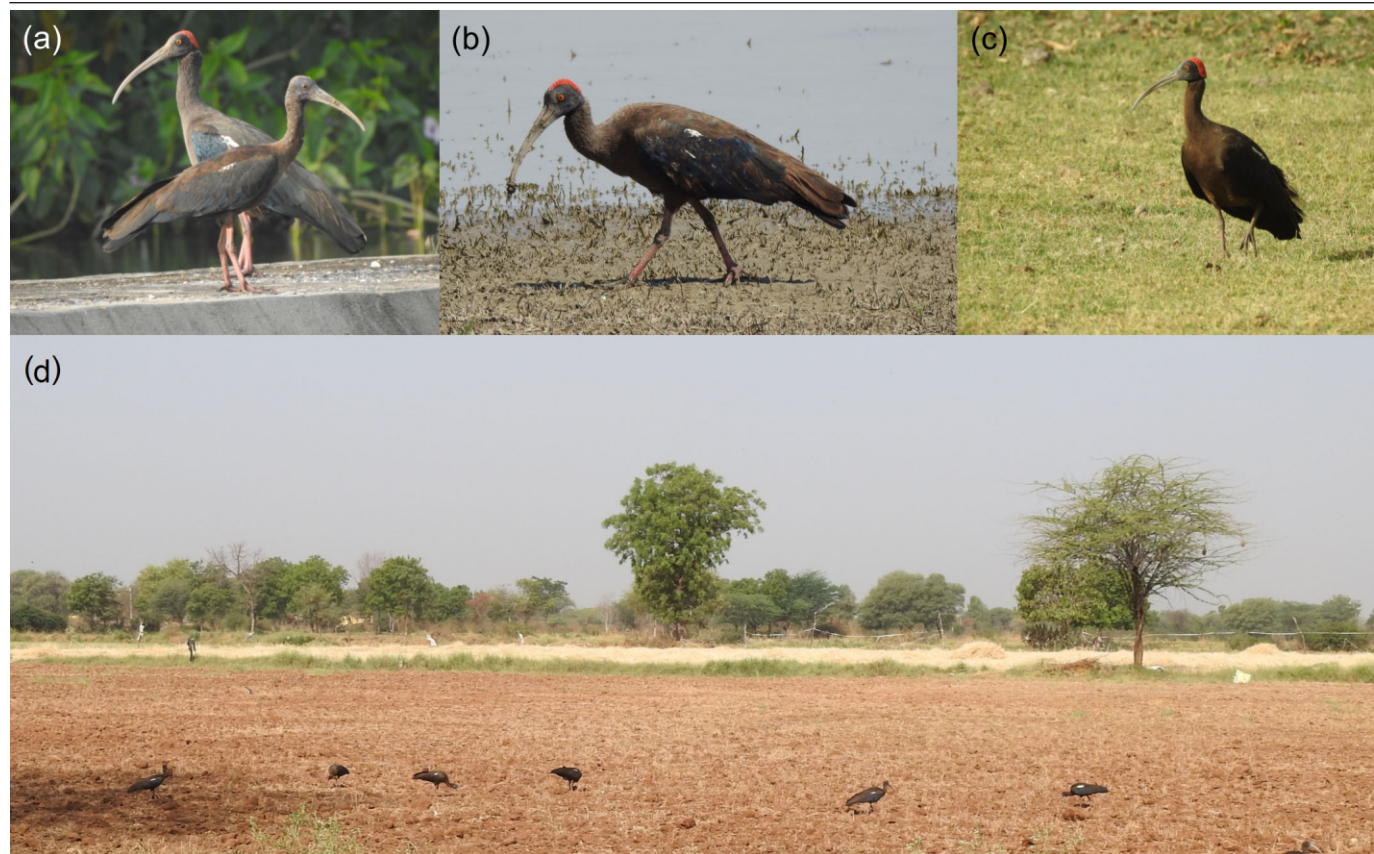
#### Analysis

We present summary metrics as average ± SD throughout the paper. Abundance of Red-naped Ibis



**Figure 1.** Location of Udaipur district in India (a), and the grid with hexagonal units of 10 km<sup>2</sup> used to overlay the district prior to selecting study locations (b). Major land uses across Udaipur district with focal hexagons (c) chosen as wetland (“water”) and agriculture hexagons are shown (d).





**Figure 2.** Photographs showing Red-naped Ibis using different habitats during field surveys in Udaipur district, Rajasthan. (a) An adult (behind) and a juvenile (in front) are standing on a cemented dyke beside a wetland; (b) an adult ibis foraging in the muddy shore of a wetland; (c) an adult ibis resting in an open grassland; and (d) an ibis flock foraging in a fallow agricultural field. Field surveys were carried out between July 2021 and May 2022. (All photographs by Hitesh Ameta.)

was estimated per hexagon as encounter rate (ibises counted/ transect length in km) for each season, as road transects were unequally distributed. We used the non-parametric permutational multivariate analysis of variance (PERMANOVA) test to assess if there were differences in flock sizes between wetland-dominated and agriculture-dominated landscapes in each season. Two-way interactions were tested between hexagon type and seasons to understand if encounter rate varied solely due to dominant land use or seasons. This test was carried out using the R-package ‘lmPerm’ with function ‘aovp’ (Wheeler and Torchiano 2016). The non-parametric test freed us from the assumption of normal data distributions. We used Fisher’s exact test in R environment to test if Red-naped Ibis sightings using individual habitat types varied across strata and seasons.

To understand if Red-naped Ibises showed preference or avoidance of individual habitat types, we employed the use-availability framework (Manly *et al.* 2004). We calculated proportions sightings of Red-naped Ibises in different habitats as “use” of each habitat and proportion of each habitat type from satellite images as “available” (Manly *et al.* 2004). Sightings in each season were contrasted against a one-time measure of habitat availability. We used function ‘widesI’ in R-packages ‘adehabitatHR’, ‘adehabitatHS’, ‘adehabitatLT’ and ‘adehabitatMA’ (Calenge 2006). The test provides log-likelihood  $\chi^2$  (or the ‘Khi2L’) value testing the hypothesis that all available habitats

were used randomly and provided selection ratios that compared use versus availability for each habitat. This allowed an assessment of whether each habitat was used more than available (preferred), or less than available (avoided), or used in proportion to availability. All statistical results were considered significant at  $p < 0.05$  level.

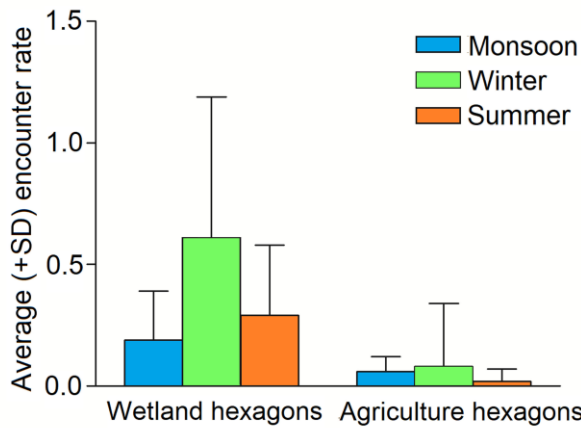
## Results

A total of 2,362 km (878 km in the monsoon season; 746 km in winter; 739 km in summer) were surveyed. The highest number of Red-naped Ibis were recorded in winter ( $N = 296$ ; 291 adults and 5 juvenile) with intermediate numbers during the monsoon ( $N = 124$ ; 102 adults, 22 juveniles), and the lowest count during the summer ( $N = 102$  adults, no juveniles).

### Encounter rate

Many more Red-naped Ibis were found in wetland hexagons in all the three seasons (monsoon:  $N = 74$ ; winter:  $N = 179$ ; summer:  $N = 114$ ) relative to agriculture hexagons (monsoon:  $N = 28$ ; winter:  $N = 39$ ; summer:  $N = 10$ ). Encounter rates (ibis seen per km in each hexagon) were magnitudes higher in wetland hexagons ( $p < 0.001$ ) especially during





**Figure 3.** Seasonal encounter rates (birds seen per km in individual hexagons) of Red-naped Ibis in wetland and agriculture hexagons in Udaipur district, Rajasthan. Field surveys were carried out from July 2021 to May 2022.

the winter ( $p < 0.001$ ; Figures 3 and 4).

#### Flock size

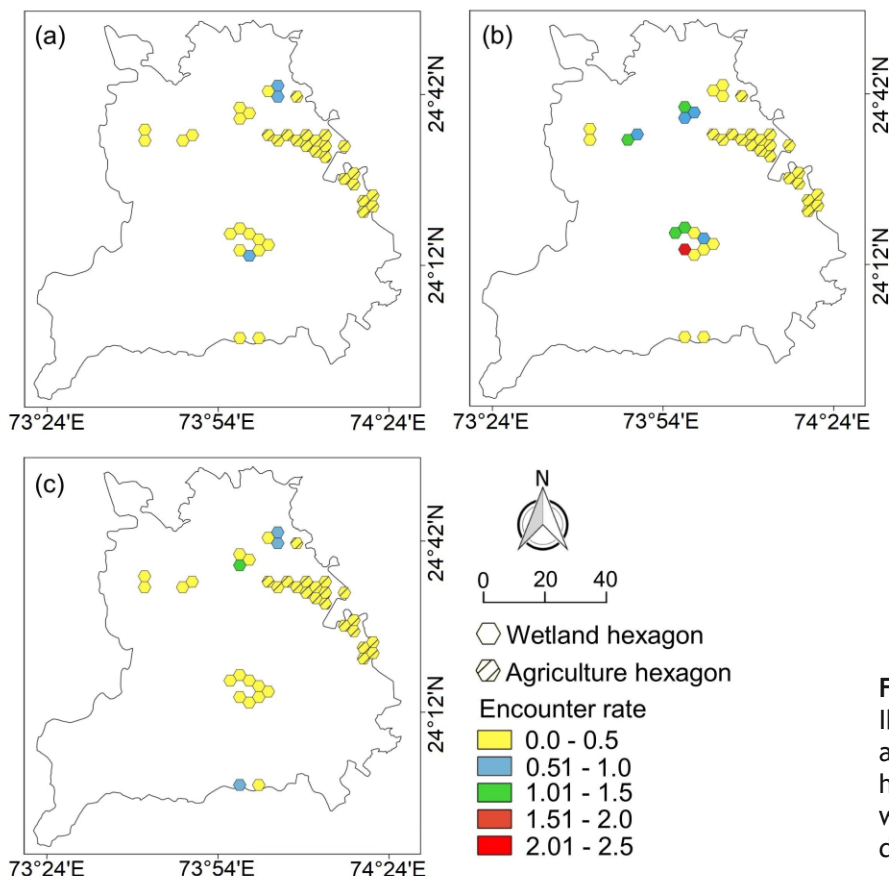
The mean flock size, combined across all hexagons, of Red-naped Ibis was magnitudes larger during the winter ( $N = 46$ ,  $6.43 \pm 11.39$  SD; range: 1 - 61 individuals) compared to the much smaller flock sizes during the summer ( $N = 41$ ,  $3.02 \pm 3.09$  SD; range: 1 - 15 individuals) and monsoon ( $N = 52$ ,  $1.96 \pm 1.52$  SD; range: 1 - 8 individuals). Most flocks comprised of  $< 5$  ibises with flocks of  $> 10$  ibises being rare and only two

observations of flocks with  $> 50$  ibises (Figure 5). Both number of flocks and sizes of individual flocks differed significantly between agricultural and wetland hexagons (Figure 5). Differences were the highest during the winter ( $p < 0.0001$ ) and summer ( $p = 0.02$ ). Flock sizes were similar in hexagons with the two dominant land uses during the monsoon despite many more ibises counted during this season relative to summer ( $p = 0.42$ ).

#### Foraging habitats

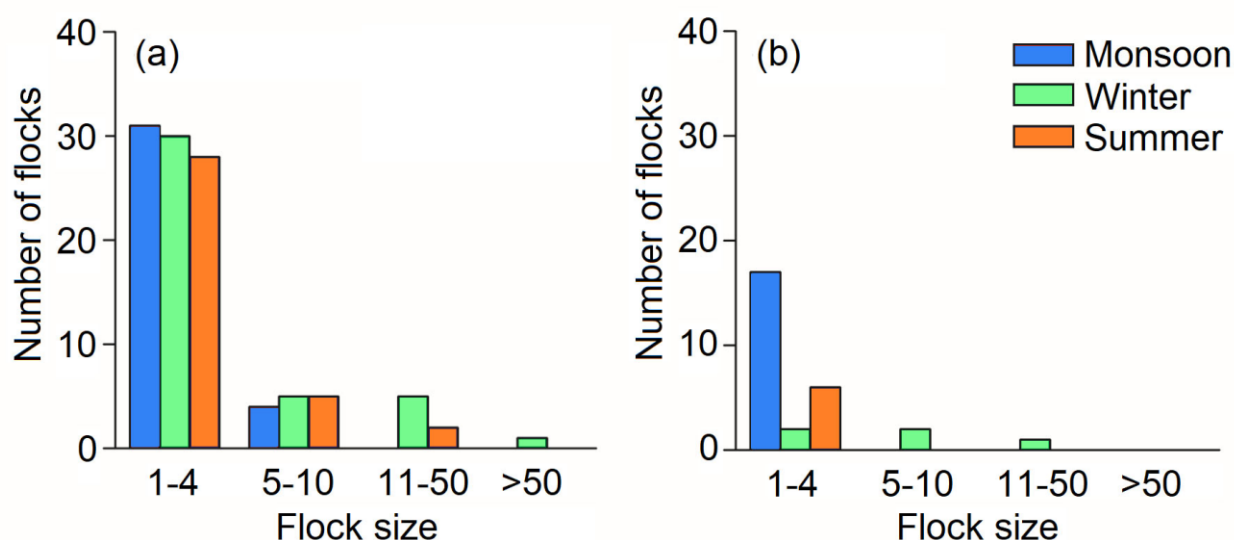
Red-naped Ibises were recorded most in the category of mixed land uses ("other", 49.23 % of total sightings— 37.3 %, 93.3 %, and 75.6 % of sightings during the monsoon, winter and summer respectively). Of the remaining sightings, the majority were observed using wetland edges (48.27 %; Figure 2b) and in built-up areas (2.49 %). Ibises were never observed using fields with standing crop. Use of different land use categories varied significantly across seasons (combining all hexagons:  $p < 0.001$ ), and within hexagons with the two dominating land uses (agriculture:  $p = 0.002$ ; wetland:  $p = 0.005$ ; Figure 6).

Considering all land use types together, Red-naped Ibises displayed very strong non-random use of categories in all seasons in both hexagon types ( $p < 0.05$ ), except during the monsoon in wetland



**Figure 4.** Encounter rates of Red-naped Ibis in wetland (without diagonal lines) and agriculture (with diagonal lines) hexagons recorded during monsoon (a), winter (b) and summer (c) in Udaipur district, Rajasthan.





**Figure 5.** Flock sizes of Red-naped Ibis in wetland (a) and agriculture (b) hexagons, in three seasons in Udaipur district, Rajasthan from July 2021 to May 2022.

hexagons ( $\chi^2 = 3.89$ ,  $p = 0.27$ ). Notwithstanding dominant land use, Red-naped Ibises strongly preferred wetlands (used more relative to availability) in all seasons (Figure 6). Built-up areas were preferred in wetland hexagons only during the monsoon, but otherwise built-up areas were used much less relative to availability (Figure 6). The category “other” was largely used less relative to availability (Figure 6).

## Discussion

Our study is the first to investigate Red-naped Ibis density, flocking and habitat use across seasons and landscape scales using an *a-priori* field design, that stratified the study area based on two dominant land uses – wetlands and agriculture. Red-naped Ibis varied seasonally in both abundance related (encounter rate) and behaviour related (flock size and habitat use) metrics, both across the full sample and between hexagons with dominant land uses. The species was mostly seen in small flocks with large aggregations being rare. Contrary to descriptions in the majority of available literature, Red-naped Ibis were strongly and positively associated with wetlands, notwithstanding the dominant land use.

### Encounter rate

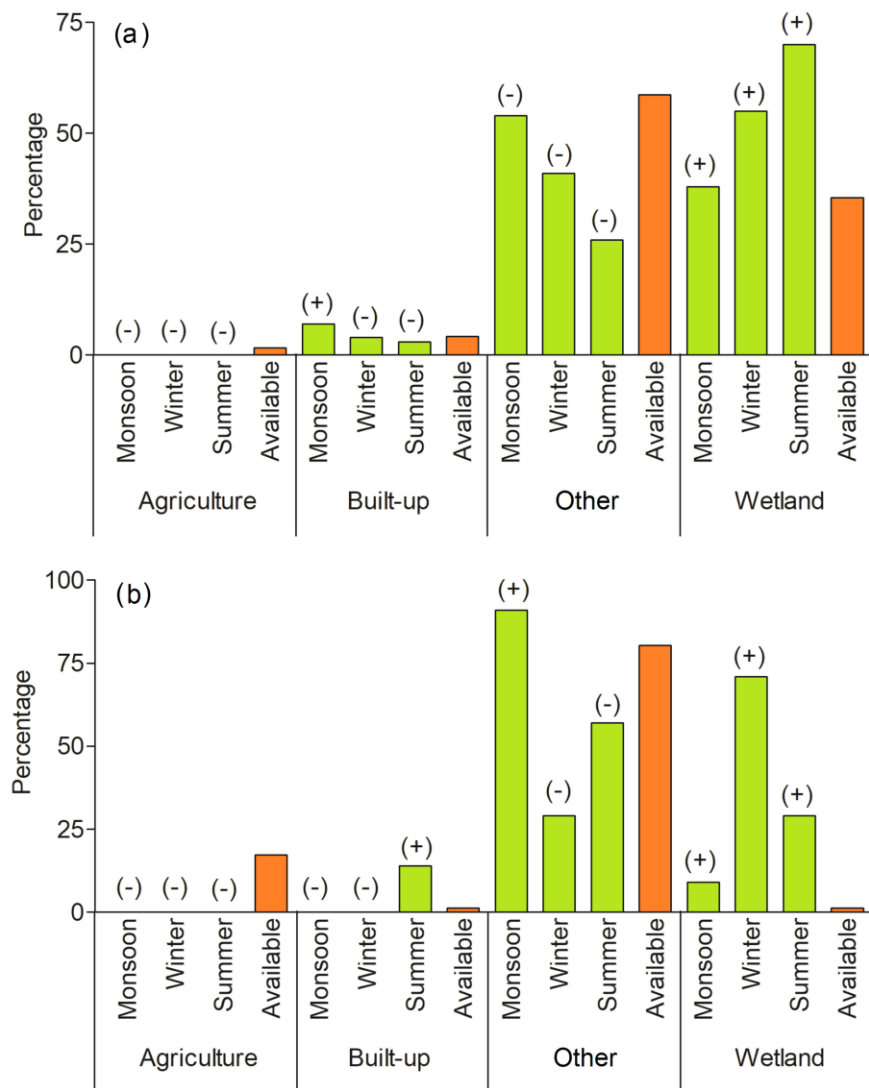
Significant differences in encounter rates of Red-naped Ibis across hexagons and seasons suggest local movements likely due to changing foraging conditions seasonally. The caveat to this explanation is that activity of ibises was not recorded for each sighting. Assuming that all

habitats were used similarly is not ideal, and future studies to parse apart habitats used for different activities will be useful. Responses of ibises, however, varied with dominant land use as indicated by encounter rates. Highest encounter rates everywhere were during the winter. However, the season with the lowest encounter rate varied between dominant land uses: monsoon in wetland hexagons, and summer in agriculture hexagons. This variation in encounter rates suggests that seasonal conditions differed as a function of dominant land use causing ibis movements in different seasons. It is also possible that breeding preferences of Red-naped Ibis varied by dominant land use, and that low encounter rates during the monsoon in wetland hexagons reflect increased activity at the nest. In north India, the breeding season for this species is thought to be March to October (summer and monsoon seasons –Ali and Ripley 2007). The addition of fledged juveniles following breeding likely contributed to higher encounter rates of Red-naped Ibis during the winter. Soni (2008) counted Red-naped Ibis at roosting sites in an arid area of Rajasthan, and found higher numbers during the winter. The two studies suggest that, most Red-naped Ibis can be counted during the winter notwithstanding the method used.

### Flock size

Red-naped Ibis mostly occurred as small flocks, matching descriptions in existing literature and more recent work where the species is described to occur largely as solitary birds, pairs, or in small family groups (Ali and Ripley 2007; Soni 2008;





**Figure 6.** Habitat use (green bars) by Red-naped Ibis and available habitat (orange bars) over three seasonal surveys in wetland-dominated (a) and agriculture-dominated (b) hexagons in Udaipur district, Rajasthan. Symbols show preference (used more relative to availability; +) and avoidance (used less relative to availability; -) of a particular habitat.

Katuwal and Quan 2022). Larger flocks with > 50 birds were rarely observed; the only sighting was during the winter in a wetland hexagon. Flock sizes varied significantly in two of three seasons due to dominant land uses (winter and summer; much larger flocks in wetland hexagons; Figure 5). This suggests that this relatively easy to measure metric is related to landscape quality but requires to be used with the caveat that flock sizes during the monsoon are likely to be similar everywhere. Previous studies have shown that Asian Openbill, Black-headed Ibis and Woolly-necked Stork flock sizes have identical variations with season (Sundar 2006; Pande *et al.* 2007; Kittur and Sundar 2020). Monsoon is a season with the highest agricultural activity in Udaipur district due to widespread availability of water and may provide additional foraging ground for the species leading to its spreading out and small flock sizes everywhere. Bigger flock sizes during the winter (particularly in wetland-dominated hexagons; Figure 5) are suggestive of newly-fledged younger Red-naped Ibis flocking in areas with more wetlands, like with other large

waterbird species (Sundar 2006; Kittur and Sundar 2021).

#### *Land use preference*

Contrary to existing literature and our hypotheses, encounter rates were far higher in wetland-dominated hexagons in all the seasons (Figures 3 and 4). Wetlands were also the most preferred habitat in all seasons in both hexagon types, and there was not a single observation of ibis in agricultural fields with standing crop (Figure 6). This finding suggests that Red-naped Ibis avoid crops in semi-arid areas such as Udaipur district. Most Red-naped Ibis were, however, seen in fallow fields (see Figure 2d). It seems likely that along with wetlands, open areas and especially fallow agricultural fields, are important for supporting Red-naped Ibis in semi-arid landscapes. Future work requires to undertake analyses related to land use more carefully and ensure that fallow agricultural land is a distinct category of land use prior to analyses relating to preference-avoidance of habitats. The importance of fallow fields as





foraging habitats has been demonstrated for a variety of waterbird species in other studies across diverse agricultural landscapes (Sundar 2006; Tscharrntke *et al.* 2011; Sundar and Kittur 2012; Toivonen *et al.* 2015). That Red-naped Ibis used fallow fields but not fields with standing crop suggests that their avoidance of fields is associated with the crops grown and not agriculture *per se*. We suspect that standing crops such as millets and maize offered physical resistance to foraging ibises, but this aspect of ibis-agriculture interaction is clearly intriguing and worthy of specific research attention. The relationship of Red-naped Ibis with built-up areas was more complex, with ibises preferring such areas in few seasons. But this seasonal preference was not similar across areas with differing dominant land uses (Figure 6). This finding is analogous to observed varying seasonal abundances of Red-naped Ibis within a small city in an arid part of Rajasthan (Soni 2008). In Udaipur, Red-naped Ibis used built-up areas much more in wetland hexagons during the monsoon, which is the primary breeding season for the species suggestive of the species relying on urban trees for breeding as in Churu, Rajasthan (Soni 2008). Why Red-naped Ibis preferred built-up areas in agricultural hexagons during the summer, and whether they entirely avoid trees found outside urban areas on the larger landscapes for breeding, are questions that are worthy of future research.

### Conclusions

Our findings show how Red-naped Ibis in semi-arid rocky regions of India interacted with different dominant land use and changed their behaviours seasonally. To fully understand species such as this ibis, studies will require to cover diverse landscapes – with rice, without rice, and other settings. We also show that Udaipur district supports a relatively large and resident population of Red-naped Ibis suggesting that areas dominated by non-rice crops also support waterbirds. Previous work in this region showed the significant importance of wetlands and urban areas in supporting a diverse assemblage and substantial abundance of foraging and roosting waterbird species (Chaudhury and Koli 2018; Koli *et al.* 2019). This work on Red-naped Ibis underscores those findings while additionally suggesting that fallow crop lands may be additionally beneficial to sustain waterbirds. Our

work adds important nuance to understanding Red-naped Ibis ecology while showcasing that this species may use somewhat different but related strategies to live alongside humans in different parts of south Asia. We underscore many recent calls to cover additional human-modified and human-dominated areas in regions such as south Asia to help uncover potentially novel settings where large waterbirds are not deterred by, but instead cope with sharp seasonal changes on the landscape accentuated by human activity.

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