



**POPULATION DYNAMICS AND BREEDING HABITAT USE BY COLONIAL
WATERBIRDS NESTING AT THE KOKKARE-BELLUR COMMUNITY RESERVE,
SOUTHERN KARNATAKA**

Thesis submitted for the award of the degree of

Doctor of Philosophy

in

WILDLIFE SCIENCE

by

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to

Saurashtra University

Rajkot- 360005 (Gujarat)

Under the supervision of

Dr. R. Suresh Kumar



**भारतीय वन्यजीव संस्थान
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DECLARATION

I, hereby, declare that the work conducted under this thesis titled “**Population dynamics and breeding habitat use by colonial waterbirds nesting at Kokkare-Bellur Community Reserve, southern Karnataka**” is a record of original and independent research work done by me and subsequently submitted for the award of the degree of **Doctor of Philosophy in Wildlife Science** to the **Saurashtra University, Rajkot (Gujarat)**. This research work has been carried out under the guidance and supervision of Dr. R. Suresh Kumar, Scientist-F, of Wildlife Institute of India, Dehradun. The work has not formed the basis for the award of any other degree, diploma or any other qualification. I also declare that the thesis embodies my own work, analysis, observation, understanding and the particulars given in it are true to the best of my knowledge.

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Miss Aksheeta Mahapatra has researched on this thesis for more than six terms under our supervision and guidance. The work presented in this thesis has not been submitted for any other degree. It meets all of the specifications stated forth in the ordinances of Saurashtra University in Rajkot, Gujarat, and the Wildlife Institute of India.

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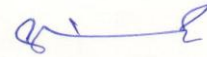
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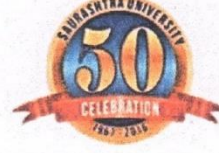
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I certify that the research work was appreciated by all who were present, and the comments made by the faculty and researchers have been appropriately included in the thesis.

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It is certified that the Ph.D. thesis entitled “POPULATION DYNAMICS AND BREEDING HABITAT USE BY COLONIAL WATERBIRDS NESTING AT THE KOKKARE-BELLUR COMMUNITY RESERVE, SOUTHERN KARNATAKA” submitted by **Aksheeta Mahapatra** has been examined by us for plagiarism check as per UGC (Promotion of Academic Integrity and Prevention of Plagiarism in Higher Educational Institutions) Regulations. The following inferences are drawn from this check:

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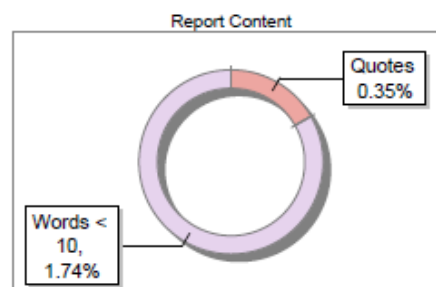
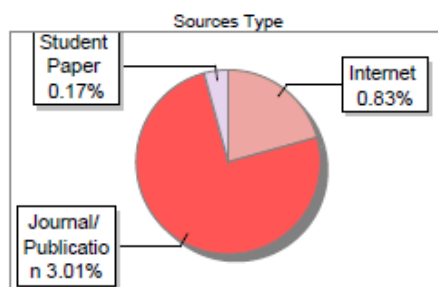
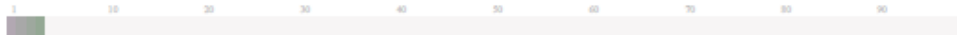
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CONTENTS

Acknowledgements	i-v
List of Figures	vi-ix
List of Tables	x-xi
List of Publications and Conferences	xii

Chapter 1.	General Introduction	1-16
Chapter 2.	Study Area	17-23
Chapter 3.	Deciphering the role of rainfall on nesting chronology at Kokkare-Bellur, Southern India a multi-species colonial nesting waterbird site	24-53
	Introduction	24-27
	Methods	28-29
	Results	29-47
	Discussion	49-52
	Conclusion	52-53
Chapter 4.	Exploring nesting niche partitioning and sharing in colonial waterbirds	54-79
	Introduction	54-57
	Methods	58-60
	Results	61-75

	Discussion	75-78
	Conclusion	78-79
Chapter 5.	Investigating the ecological dynamics influencing the nest survival rate in colonial waterbird species nesting at Kokkare-Bellur	80-107
	Introduction	80-82
	Methods	83-86
	Results	86-102
	Discussion	103-106
	Conclusion	106-107
Chapter 6.	Foraging habitat dynamics and ranging patterns of the Spot-billed Pelican during the breeding and non-breeding phases	108-123
	Introduction	108-109
	Methods	110-112
	Results	112-120
	Discussion	120-123
Chapter 7.	Conclusion: Conservation and Management of waterbirds at Kokkare-Bellur	124-129
Literature cited		130-144
Annexure		145-169

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LIST OF FIGURES

Figure	Caption	Page No.
Figure 2.1	(a) Kokkare-Bellur, situated in southern Karnataka in peninsular India, (b) Village boundary bounded by Shimsha River from the west, and (c) Centre region of the village and tree patches used for nesting by the waterbirds.	19
Figure 3.1	Nesting patterns of waterbirds (Spot-billed Pelican, Painted Stork, Black-crowned Night Heron, Little Egret, Little Cormorant: arranged in body size gradient from top to bottom) at Kokkare-bellur Community Reserve from October 2018 - September 2023. Σ value represents total rainfall in mm recorded in a particular year. N is the number of active nests for a specific breeding season.	30
Figure 3.2	Variation in nest initiation dates of Spot-billed Pelican in Kokkare-Bellur during 2018-23.	32
Figure 3.3	Variation in nest initiation dates of Painted Stork in Kokkare-Bellur during 2019-23.	33
Figure 3.4	Variation in nest initiation dates of Black-crowned Night Heron in Kokkare-Bellur during 2019-23.	34
Figure 3.5	Variation in nest initiation dates of Little Egret in Kokkare-Bellur during 2019-23.	35
Figure 3.6	Variation in nest initiation dates of Little Cormorant in Kokkare-Bellur during 2019-23.	36
Figure 3.7	Box plot showing interannual variation of nesting duration for different waterbird species nesting at Kokkare-Bellur, (a) Spot-billed Pelican (b) Painted Stork (c) Black-crowned Night Heron (d) Little Egret (e) Little Cormorant. The thick horizontal stroke inside the box shows the median, the box represents the interquartile range, the vertical line extending from the box represents standard deviation. # For Night Heron, Little Egret and Little Cormorant, data was not collected for the 2018-19 breeding season.	38
Figure 3.8	Inter-species variation in nesting success across the five breeding seasons for (a) Spot-billed Pelican (b) Painted Stork (c) Black-crowned Night Heron (d) Little Egret (e) Little Cormorant.	42
Figure 3.9	Inter-species variation in nesting success when there were multiple nesting events in a single nesting season. In the box below the value of N represents	44

	the total number of active nests during the multiple nesting events in a particular breeding season.	
Figure 3. 10	Box plot of inter-species variation in the number of chicks fledged per nest for (a) Spot-billed Pelican (b) Painted Storks (c) Black-crowned Night Heron (d) Little Egret (e) Little Cormorant, across the five breeding seasons. The thick horizontal stroke inside the box shows the median, the box represents the interquartile range, the vertical line extending from the box represents standard deviation. Data for Night Heron, Egret and Cormorant for 2018-19 season was not recorded.	46
Figure 4. 1	Clustering of nesting trees based on spatial coordinates using k-means. Each color represents a distinct species and distinct shape represent spatial cluster.	62
Figure 4. 2	Spatial context and species-specific nesting space use of colonial waterbirds in Kokkare-Bellur village. (a) Google Earth image of Kokkare-Bellur village, providing spatial context for the nesting tree patches. Panels (b–f) show kernel density estimation (KDE) heatmaps representing species-specific nesting space use within the village, where darker shading indicates higher nest density. Species shown are: (b) Little Cormorant, (c) Little Egret, (d) Black-crowned Night Heron, (e) Painted Stork, and (f) Spot-billed Pelican.	64
Figure 4. 3	NMDS ordination of nesting tree sites based on the presence of five colonial waterbird species- Little Cormorant, Little Egret, Black-crowned Night Heron, Painted Stork, and Spot-billed Pelican, via Jaccard dissimilarity. Points represent individual nesting trees, while colored ellipses (95% confidence intervals) indicate species-specific clustering and overlap in nesting habitat use. Arrows denote the five most influential environmental variables fitted using envfit, with arrow length proportional to the strength of correlation with the ordination axes. The ordination is displayed in two dimensions ($k = 2$); stress value indicates the goodness-of-fit of the NMDS solution.	68
Figure 4. 4	Species-specific forest plots showing nesting tree preferences of five colonial waterbird species. Odds ratios (with 95% confidence intervals) from Firth's logistic regression indicate the relative likelihood of nest occurrence on different tree species for (a) Little Cormorant, (b) Little Egret, (c) Black-crowned Night Heron, (d) Painted Stork, and (e) Spot-	71

	billed Pelican. The vertical dashed line denotes an odds ratio of 1 (no effect).	
Figure 4. 5	Variation in nearest neighbor distance (NND, m) among five waterbird species. Boxplots indicate the median and interquartile range, with points representing individual nest-level observations.	73
Figure 4. 6	Differences in nest density (number of nests per tree) among five waterbird species. Boxplots indicate the median and interquartile range, and points show tree-level observations.	74
Figure 4. 7	Vertical stratification of nesting, expressed as nest height (m), among five waterbird species. Boxplots represent the median and interquartile range, with points indicating individual nest observations.	75
Figure 5. 1	Model-predicted effects of ecological, temporal, and climatic variables on nest failure probability in Spot-billed Pelicans. Panels show the predicted probability of nest failure as a function of (a) cluster size, (b) nest density, (c) nest height, (d) nest initiation date, and (e) total precipitation. Shaded bands represent 95% confidence intervals.	91
Figure 5. 2	Model-predicted effects of climatic and phenological variables on nest failure probability in Painted Storks. Panels show predicted probabilities as a function of (a) minimum temperature, (b) total precipitation, and (c) nest initiation date based on the best-supported model. Shaded bands represent 95% confidence intervals.	94
Figure 5. 3	Model-predicted effects of colony structure, landscape context, nesting phenology, and climatic variables on nest failure probability in Black-crowned Night Herons. Panels show predicted probabilities as a function of (a) colony area, (b) distance to built-up areas, (c) nest density, (d) nest initiation date, (e) minimum temperature, and (f) total precipitation based on the best-supported model. Shaded bands represent 95% confidence intervals.	97
Figure 5. 4	Model-predicted effects of nesting phenology, and climatic variables on nest failure probability in Little Egret. Panels show predicted probabilities as a function of (a) nest initiation date, and (b) total precipitation based on the best-supported model. Shaded bands represent 95% confidence intervals.	99
Figure 5. 5	Model-predicted effects of colony structure, nesting phenology, and climatic variables on nest failure probability in Little Cormorant. Panels show predicted probabilities as a function of (a) colony area, (b) nest	102

	initiation date, and (c) total precipitation based on the best-supported model. Shaded bands represent 95% confidence intervals.	
Figure 6. 1	Utilization distributions (UD) of the juvenile Spot-billed Pelican (Shimsha) derived from Dynamic Brownian Bridge Movement Models (dBBMM). The maps show the 50% (core), 75% (primary), and 99% (overall) UD for (a) the first-year post-release (November 2022–November 2023) and (b) the second-year post-release (November 2023–November 2024), illustrating spatial expansion over time. Note that both maps are on independent scales.	114
Figure 6. 2	Non-breeding season utilization distributions (UD) of the adult Spot-billed Pelican (Aadi) derived from Dynamic Brownian Bridge Movement Models (dBBMM). The maps show a comparison between (a) the first non-breeding season (February–September 2023), characterized by wide-ranging movements across the Bengaluru-Mysuru corridor, and (b) the second non-breeding season (May–September 2024), showing a dramatic contraction and refinement of the core use areas around Mysuru. Note that both maps are on independent scales.	116
Figure 6. 3	Inter-annual comparison of breeding season space use for the adult Spot-billed Pelican (Aadi). The dBBMM utilization distributions (UDs) show (a) an extensive home range (99% UD: 703 km ²) during the first breeding season (October 2023–April 2024), encompassing two nesting attempts. This is contrasted with (b) a more efficient, contracted home range (99% UD: 471 km ²) in the second breeding season (October 2024–February 2025), reflecting site fidelity to the successful Ranganathittu colony and the elimination of exploratory movements. Note that both maps are on independent scales.	118
Figure 6. 4	Comparison of age-dependent movement patterns in two Spot-billed Pelicans tracked using GPS telemetry. The juvenile (Shimsha) shows a progressive increase in daily distance travelled over time, whereas the adult (Aadi) exhibits a cyclical movement pattern with pronounced peaks in daily travel during breeding seasons, consistent with central-place foraging behaviour. Vertical dashed lines indicate the onset and termination of Aadi's breeding periods (October 2023–April 2024 and October 2024–February 2025). Lines represent LOESS-smoothed mean daily distance travelled, with shaded bands indicating 95% confidence intervals.	120

LIST OF TABLES

Table	Caption	Page No.
Table 3.1	Poisson regression coefficients for nesting duration for different waterbird species across the different nesting season. Year 1 = 2018-19 breeding season, Year 2 = 2019-20 breeding season, Year 3 = 2020-21 breeding season, Year 4 = 2021-22 breeding season, Year 5 = 2022-23 breeding season.	39-40
Table 3.2	Pearson Chi-Square values for nesting success variation of waterbirds across the breeding seasons.	43
Table 3.3	Fisher's Exact Test for nesting success variation of smaller waterbirds across the multiple nesting events during different breeding seasons.	44-45
Table 3.4	Poisson regression coefficients (vglm) for nesting duration for different waterbird species across the different nesting season. Year 1 = 2018-19 breeding season, Year 2 = 2019-20 breeding season, Year 3 = 2020-21 breeding season, Year 4 = 2021-22 breeding season, Year 5 = 2022-23 breeding season.	47-48
Table 4.1	Species-wise distribution of trees recorded at Kokkare-Bellur village, categorized by presence and absence of colonial waterbird nesting activity, indicating relative nesting preference across tree species.	66-67
Table 5.1	Inter-annual variation in nesting success, fledgling production, and stage-specific nest failure of five colonial waterbird species at Kokkare-Bellur (2018–2023). NF stages indicate the developmental stage at which nest failure occurred: Stage 1 = nest building, Stage 2 = incubation, Stage 3 = young chick mortality, Stage 4 = old chick mortality.	87-88
Table 5.2	Summary of best-fit GLMM models predicting nesting failure for five colonial waterbird species at Kokkare-Bellur. All models include 'Year' as a random intercept. This table shows only the statistically significant predictors ($p < 0.05$) and their estimated effects.	89
Table 5.3	AICc-based model selection evaluating temporal, climatic, nest-site, anthropogenic, and colony-level predictors of nest failure in Spot-billed Pelican. The full model included nest initiation timing, climatic variables (minimum temperature and total precipitation), nest-site characteristics (nest height, nearest-neighbor distance, nest density, and cluster size),	92-93

	anthropogenic proximity (distance to road and distance to built-up area), and colony area.	
Table 5. 4	AICc-based model selection identifying key determinants of nest failure in Painted Stork. Candidate models assessed the influence of nest initiation timing, climatic conditions (minimum temperature and total precipitation), nest-site attributes (nest height, nearest-neighbor distance, and nest density), anthropogenic proximity, and canopy area. Models within $\Delta AICc \leq 2$ are considered to have substantial empirical support.	94-96
Table 5. 5	Model selection results for predictors influencing nest failure in Black-crowned Night Heron using AICc. Models evaluated the relative importance of temporal, climatic, nest-site, anthropogenic, and colony-level variables, including nest initiation timing, temperature, precipitation, nest density, proximity to built-up areas, and colony area. Lower AICc values indicate better-supported models.	98-99
Table 5. 6	AICc-based model selection assessing factors affecting nest failure in Little Egret. Candidate models examined the effects of nest initiation timing, climatic variables, nest-site characteristics, anthropogenic proximity, and colony area. Predictor combinations are ranked according to AICc, with $\Delta AICc$ reflecting relative model support.	100-101
Table 5. 7	AICc-based model selection evaluating drivers of nest fate in Little Cormorant. Models assessed the influence of temporal (nest start day), climatic (minimum temperature and total precipitation), nest-site, anthropogenic, and colony-level variables. The best-supported models highlight the relative contribution of colony area and climatic timing effects on nesting outcomes.	102

LIST OF PUBLICATION AND CONFERENCES

Peer-reviewed Publications (Annexure 1)

1. **Mahapatra, A.** (2026). Spotting the difference: Sexual size dimorphism and individual identification in the Spot-billed Pelican *Pelecanus philippensis*. Journal of Wildlife Science (Accepted) [ISSN (online): 3048-7803]
2. **Mahapatra, A.**, and Kumar, R.S. (2026). Nest partitioning in a mixed-species waterbird colony in a human-dominated landscape of Southern India. Journal of Field Ornithology (in review) [ISSN: 1557-9263]
3. **Mahapatra, A.**, Baraiya, H.L., and Kumar, R.S. (2026). Post-release dispersal, space use, and breeding integration of rescued adult and juvenile Spot-billed Pelicans tracked using GPS telemetry. Journal of Wildlife Science (in review) [ISSN (online): 3048-7803]

Conference (Annexure 2)

- International
1. Birds of different feather also flock together: Spatial and temporal nesting patterns in a mixed species heronry in southern India. November 9-12, 2021. Waterbird Society, 45th Annual Meeting, Virtual Meeting.
 2. Changing times and changing attitudes: Spot-billed Pelican *Pelecanus philippensis* conservation at Kokkare-Bellur Community Reserve. November 6-9, 2019. Pelicans of the World Symposium, Waterbird Society, 43rd Annual Meeting, Maryland, USA.
- National
1. Changing times and changing attitudes: Spot-billed Pelican *Pelecanus philippensis* conservation at Kokkare-Bellur Community Reserve. December 7-10, 2019. National Symposium on Avian Biology, IISER Tirupati, India.

Chapter – 1

GENERAL INTRODUCTION

1.1 The Ecological Significance and Conservation of Colonial Waterbirds

Waterbirds, a functionally diverse assemblage of species inextricably linked to aquatic ecosystems, represent some of the most conspicuous and ecologically vital components of global biodiversity. Their presence, abundance, and reproductive success serve as critical barometers of the health of wetlands, reflecting subtle and overt changes in water quality, habitat integrity, food web dynamics, and the pervasive impacts of global climate change (Amat and Green, 2009). Among these species, a significant proportion, approximately one in eight avian species worldwide, exhibits a gregarious breeding strategy known as coloniality (Rolland *et al.* 1998). This behavior involves individuals congregating in dense aggregations, which can range from a few pairs to many tens of thousands, to nest and rear their young in close proximity (Wittenberger and Hunt, 1985; Brown and Brown, 2001). This life-history strategy is particularly prominent among families such as Pelecanidae, Phalacrocoracidae, Ardeidae, Ciconiidae, and Threskiornithidae (Wetlands International, 2023). These species frequently form large, multi-species colonies, commonly referred to as 'heronries,' 'rookeries,' or 'pelicanries,' which function as dynamic, ephemeral hubs of intense biological activity (Subramanya, 1996; Urfi, 2011).

The evolution and maintenance of colonial nesting present a classic evolutionary paradox, representing a complex and perpetual trade-off between substantial fitness benefits and equally significant costs (Wittenberger and Hunt, 1985). The primary selective advantages of group living are widely considered to be twofold: enhanced defense against predation and increased foraging efficiency. Densely packed colonies can effectively deter predators through several

mechanisms. Collective vigilance, encapsulated in the 'many eyes' hypothesis, increases the probability of early predator detection, allowing for a more rapid and coordinated response (Beauchamp, 2015). Active, communal defense strategies, such as mobbing, can harass and drive away potential threats far more effectively than individual efforts. Furthermore, the sheer density of nests can create a 'predator swamping' or dilution effect, where the per-capita risk of predation for any single nest is statistically reduced (Minias and Kaczmarek, 2013). For species that exploit unpredictable and patchily distributed food resources, colonies are theorized to function as 'information centers.' In this model, unsuccessful foragers can observe and follow successful conspecifics to rich feeding grounds, thereby optimizing energy expenditure and reducing the uncertainty associated with locating ephemeral resources (Ward and Zahavi, 1973; Danchin and Wagner, 1997).

Conversely, high-density aggregations impose considerable ecological and social costs that can negatively impact individual fitness. The congregation of numerous individuals inevitably leads to intensified intraspecific and interspecific competition for limited, high-value resources. This competition is particularly acute for prime nesting sites that offer greater stability and protection, for access to limited nesting materials, and for food resources in the foraging grounds surrounding the colony (Burger, 1979; Cuthill and Houston, 1997). The close physical proximity of individuals also elevates the risk of epizootic events, facilitating the rapid transmission of diseases and parasites, which can lead to catastrophic, colony-wide mortality events (Brown and Brown, 2004). Indeed, such events have been documented in Indian heronries, including the mass mortality of Spot-billed Pelicans at Kokkare-Bellur linked to parasitic nematode infestations (Kumar *et al.* 2018). Furthermore, the constant social interactions, including territorial disputes, kleptoparasitism (food theft), and extra-pair copulation attempts, can induce chronic physiological stress, which may compromise immune function and ultimately reduce reproductive output (Anderson, 2006). The decision to nest

colonially is thus a finely balanced outcome of these conflicting selective pressures, shaped by a species' unique life history, the local predator landscape, and the spatiotemporal distribution of its essential food resources.

Despite their ecological resilience, colonial waterbird populations are facing a precipitous and well-documented global decline (Wetlands International, 2023). This alarming trend is mirrored in the Indian subcontinent, as highlighted by successive 'State of India's Birds' reports, which underscore significant long-term declines and range contractions for many wetland-dependent species (SoIB, 2023b). The primary drivers of this decline are overwhelmingly anthropogenic in nature. The relentless destruction and degradation of wetland habitats, primarily through drainage for agricultural expansion, urban development, and industrialization, represent the most pervasive and immediate threat. This habitat loss shrinks the available area for both nesting and foraging, fragments populations, and disrupts essential hydrological processes (Davidson, 2014). Environmental contamination is a more insidious, but equally potent, threat. Pesticides, heavy metals, and industrial effluents accumulate in water bodies and bioaccumulate through aquatic food webs, leading to direct toxicity, endocrine disruption, eggshell thinning, and reproductive failure in top predators like large waterbirds (Pandiyan *et al.* 2022). The ubiquitous threat of plastic pollution poses a further risk through ingestion, leading to internal injury and starvation, and entanglement, which can cause drowning or severe physical impairment.

Superimposed on these direct pressures is the overarching and accelerating threat of climate change. Altered climatic patterns disrupt established hydrological regimes, leading to more frequent and intense droughts and floods. These changes can cause critical temporal mismatches between waterbird breeding phenology and the availability of their prey, leading to widespread nesting failure (Spalding *et al.* 2010). Furthermore, the increased frequency and

intensity of extreme weather events, such as cyclonic storms and unseasonal heavy rainfall, can physically devastate nesting colonies, leading to the destruction of nests and direct mortality of eggs and chicks. Finally, direct human disturbance such as from recreational activities like boating, unregulated fishing practices, and intrusive tourism, can cause adult birds to flush from their nests, leading to nest abandonment and leaving vulnerable eggs and chicks exposed to predation and lethal thermal stress (Rodgers Jr. and Smith, 1997; Carney and Sydeman, 1999). Given their high trophic position, their sensitivity to environmental change, and the myriad threats they face, the study of colonial waterbird ecology is not merely an academic pursuit but a fundamental conservation imperative. A deep and nuanced understanding of the complex factors that govern their population dynamics, community structure, and reproductive success is fundamental to developing effective, evidence-based strategies to safeguard these magnificent species and the vital wetland ecosystems they inhabit.

1.2 Breeding in Human-Dominated Landscapes: The Indian Context

The ecological dynamics of colonial waterbirds exhibit profound variation across latitudinal gradients. In temperate zones, the timing of breeding is often precisely synchronized by predictable seasonal cues such as increasing photoperiod and temperature, which reliably signal the forthcoming spring pulse of resources and peak food availability for provisioning young (Crick, 2004). In tropical regions, however, where seasonal temperature and daylight fluctuations are less pronounced, rainfall emerges as the paramount environmental driver of ecosystem productivity (Stutchbury and Morton, 2001). In the Indian subcontinent, the onset, intensity, and duration of the Southwest and Northeast monsoons directly govern wetland hydrology. These rains replenish rivers, fill irrigation tanks and village ponds, and inundate vast tracts of agricultural land, which in turn dictates the productivity and accessibility of aquatic prey such as fish, amphibians, and invertebrates (Frederick and Loftus, 1993). This

monsoonal pulse of resources is the primary ultimate factor timing the breeding chronology of most of India's colonial waterbirds, whose reproductive success is inextricably linked to their ability to synchronize the energetically demanding periods of egg-laying and chick-rearing with this period of peak food availability (Urfi, 2011; Tiwary and Urfi, 2016).

The Indian subcontinent, with its diverse climatic zones and extensive network of natural and man-made wetlands, supports a rich diversity of waterbirds and hosts some of the world's most significant heronries. Seminal work by Subramanya (1996) provided the first comprehensive documentation of Indian heronries, cataloging over 300 sites and revealing that their distribution is non-uniform, concentrated in regions with abundant wetland habitats and safe nesting substrates. This work laid the foundation for decades of subsequent research. Studies have explored various facets of heronry ecology, including population monitoring (Manakadan and Kannan, 2003), the ecological role of specific sites like the Delhi Zoo heronry, and the conservation status of flagship species like the Painted Stork (Urfi, 2011, Tiwary and Urfi, 2016). Research has also begun to delve into the finer aspects of community ecology, such as interspecific interactions and niche partitioning. For example, recent work by Abbasi and Khan (2023) in northern India demonstrated fine-scale spatial, temporal, and trophic niche partitioning among four sympatric egret species, highlighting how even morphologically similar species can coexist by minimizing resource overlap. Similarly, a study by Frank *et al.* (2021) in southern India found that nesting-tree characteristics, particularly height and canopy structure, governed the vertical and spatial segregation of nests, emphasizing the role of habitat structure in maintaining colony diversity.

A particularly striking feature of the tropical Asian conservation landscape, and a central theme of this thesis, is the high prevalence of waterbird colonies situated not in remote, protected wilderness, but within or immediately adjacent to human-dominated agricultural and village landscapes (Subramanya, 1996; Urfi, 2011). This close and often ancient association presents

a unique conservation paradigm fraught with both intensified threats and novel opportunities. On one hand, proximity to human settlements exposes birds to heightened levels of chronic disturbance, the progressive loss of large, mature nesting trees for urban expansion and agriculture, and pollution from untreated sewage and agricultural runoff (Manakadan and Kannan, 2003; Sundar, 2004). Research indicates that while some common, generalist waterbird species may benefit from certain anthropogenic landscapes (e.g., irrigated paddy fields), many threatened and specialist species often experience population declines in such modified habitats, highlighting that these areas are not always effective surrogates for natural wetlands.

On the other hand, a long and rich history of cultural tolerance and protection has allowed many of India's most important heronries to persist, and even thrive, for centuries within the heart of human settlements (Subramanya, 1996; Kannan, 2023). Sites like Kokkare-Bellur in Karnataka, Koonthankulam in Tamil Nadu, and Uppalapadu in Andhra Pradesh challenge the conventional temperate-zone conservation paradigm, where anthropogenic presence and disturbance are almost universally linked to reduced nest success and colony abandonment (Carney and Sydeman, 1999). In these unique South Asian socio-ecological systems, the continuous presence of humans may inadvertently create a "human shield" or "predator refuge" effect. This phenomenon occurs when natural predators that exhibit greater avoidance of human activity are deterred from approaching the colony, thereby inadvertently increasing the nesting success of birds that have adapted to and habituated these environments (Tryjanowski *et al.* 2013; Abbasi and Khan, 2023). This dynamic is exemplified in numerous community-protected sites across India, where birds are not just tolerated but are actively revered, protected, and integrated into the local cultural and spiritual identity.

However, this traditional tolerance is not static and is eroding rapidly under the immense pressures of globalization, rapid urbanization, changing lifestyles, and shifting socio-economic

aspirations (Manu and Jolly, 2000). The symbiotic relationships that once defined these systems are becoming increasingly fragile. Consequently, there is a critical knowledge gap and an urgent conservation need to understand the complex ecological mechanisms that permit diverse, multi-species waterbird assemblages to successfully breed under these complex and often conflicting pressures. Comprehensive, long-term, multi-species studies are particularly lacking, making it difficult to discern whether the factors driving reproductive success are universal across all species in a colony, or if coexistence is facilitated by divergent, species-specific strategies for navigating the unique challenges and opportunities of a human-inhabited landscape. Answering these fundamental questions is paramount for the holistic conservation of entire heronry communities, which are simultaneously critical biodiversity hotspots and living, albeit threatened, models of human-wildlife coexistence.

1.3 The Study System: Kokkare-Bellur Community Reserve – A Natural Laboratory for Avian Ecology and Conservation

Among the hundreds of heronries documented across the Indian subcontinent (Subramanya, 1996), the Kokkare-Bellur Community Reserve (KBCR) in Mandya District, Karnataka, stands out as a globally unique and ecologically significant site. Its very name, a portmanteau of *Kokkare* (the local Kannada name for the Painted Stork) and *Bellur* (the name of the village, also meaning 'white village,' perhaps alluding to the bird droppings), encapsulates the village's identity, which has been inextricably intertwined with its annual avian visitors for centuries. Formally designated as Karnataka's first Community Reserve in 2007 under Section 36C of the Wildlife (Protection) Act, 1972, KBCR defies the conventional definition of a protected area (Neginhal, 1977). It is not a secluded, government-managed sanctuary, instead, it is an inland, mixed-species heronry nestled entirely within the dynamic matrix of a living human settlement, where the large, traditional nesting trees are scattered across private residential

backyards, school grounds, temple premises, and the bunds of agricultural plots (Manu and Jolly, 2000). This intimate spatial arrangement makes it a quintessential example of a human-dominated ecosystem and a powerful, living "natural laboratory" for investigating the core themes of this doctoral thesis.

The historical relationship between the villagers of Kokkare-Bellur and the birds, particularly the flagship Painted Storks (*Mycteria leucocephala*) and the globally Near Threatened Spot-billed Pelicans (*Pelecanus philippensis*), is a celebrated example of symbiotic coexistence. For generations, villagers have traditionally regarded the arrival of the birds as an auspicious event, harbingers of good fortune and timely rains, and have affectionately referred to them as "daughters of the village" who return to their maternal home each year to give birth and raise their young (Neginhal, 1977; Manu and Jolly, 2000). In return for this cultural protection, the nutrient-rich guano from the nesting birds was systematically collected and used as a valuable natural fertilizer for local crops, primarily sugarcane and finger millet. This deep-rooted cultural ethos has fostered a unique climate of tolerance and active protection that has allowed the heronry to persist for generations, offering a rare and invaluable opportunity to study the long-term ecological dynamics of colonial waterbirds in a landscape continuously shaped by and integrated with human presence.

The ecological context of KBCR is as compelling as its social one. Geographically, it is situated in the semi-arid rain-shadow region of the Western Ghats, a landscape characterized by moderate and highly variable annual rainfall delivered primarily by the Southwest (June-September) and Northeast (October-December) monsoons (Shilpashree *et al.* 2016). The heronry itself is not located within or adjacent to a large, permanent wetland. Instead, the breeding birds depend entirely on a dispersed network of external waterbodies for foraging. This foraging landscape includes the nearby Shimsha River, a mosaic of dozens of small- to medium-sized irrigation tanks (*keres*), and thousands of hectares of seasonally flooded paddy

fields. This complex and dynamic landscape mosaic of dryland crops, irrigated agriculture, and scattered wetlands creates a challenging environment where food resource availability is tightly and directly coupled with the unpredictable patterns of monsoonal rainfall.

This unique socio-ecological system provides an exceptional and unparalleled research platform for several critical reasons. First, it allows for the investigation of fundamental questions in breeding ecology within a system where anthropogenic factors are not merely external disturbances to be controlled for, but are integral, structural components of the habitat itself. Second, the presence of a diverse, multi-species breeding assemblage with a wide gradient of body sizes, foraging ecologies, and conservation statuses enables a powerful comparative approach to understanding mechanisms of niche partitioning and differential species responses to shared environmental pressures. Third, the site faces a pressing suite of contemporary conservation challenges that mirror those occurring in other human-dominated landscapes across Asia. These include the progressive loss of large, mature nesting trees to road widening and infrastructure development, a decline in traditional community engagement due to changing socio-economic values, and emerging epizootic threats, such as the parasitic nematode infestations that caused mass mortality of pelicans in 2015-2018 (Kumar *et al.* 2018). Studying how the five focal species of this thesis navigate the complex web of opportunities (e.g., the "human shield" effect) and constraints (e.g., resource unpredictability) of this system is therefore not only of fundamental ecological interest but also of profound and direct importance for applied conservation. This thesis leverages the unique attributes of Kokkare-Bellur to systematically dissect the intricate interplay of climate, social context, landscape structure, and species-specific ecology in shaping the population dynamics and reproductive success of colonial waterbirds.

1.4 Target species (Spot-billed Pelican, Painted Stork, Black-crowned Night Heron, Little Egret, Little Cormorant)

This thesis adopts a multi-species approach, focusing on a representative assemblage of five colonial waterbird species that breed sympatrically at Kokkare-Bellur. These species were selected to span a broad gradient of body sizes, foraging strategies, conservation statuses, and phenological timings, providing a robust framework for a comparative analysis of community ecology and interspecific dynamics within the heronry.

Spot-billed Pelican (*Pelecanus philippensis*)

Classified as Near Threatened on the IUCN Red List, the Spot-billed Pelican is a species of high regional and global conservation concern. Its populations have suffered significant declines due to the widespread loss and degradation of wetlands, water pollution, and persistent disturbance at its few remaining breeding colonies (Kannan, 2023). In India, it is a localized breeder, with nesting recorded at only about 20 sites, the majority of which are in the southern states of Andhra Pradesh, Karnataka, and Tamil Nadu, making Kokkare-Bellur a crucial stronghold for the species (Kannan and Pandiyan, 2012). Its breeding season is protracted, typically commencing with the end of the Southwest Monsoon in October and extending through April or May. As a large-bodied (152 cm), obligate piscivore, it is an apex predator in the aquatic food web and a sensitive indicator of wetland health and fish stock availability (Amat and Green, 2009). It forages cooperatively by swimming and scooping fish in its large gular pouch, typically in deeper, open water bodies. Its strict reliance on very large, stable trees for establishing its bulky nests and its vulnerability to both direct and indirect threats make it a key flagship species for conservation efforts at Kokkare-Bellur and across its range.

Painted Stork (*Mycteria leucocephala*)

The Painted Stork is a large (102 cm), strikingly colorful wading bird, currently listed as Least Concern by the IUCN. It is the namesake of Kokkare-Bellur (*Kokkare*) and is numerically the most dominant breeding species at the site, with hundreds of pairs nesting annually (Choudhary, 2025). This species is a specialist tactile forager, feeding by slowly wading through shallow water and sweeping its partially open, sensitive bill from side to side to detect and capture fish, amphibians, and large aquatic invertebrates. In India, it breeds in colonies across the country, with major sites in Keoladeo National Park (Rajasthan), Ranganathittu Bird Sanctuary (Karnataka), and numerous sites in Gujarat and Uttar Pradesh (Urfi, 2011; Tiwary and Urfi, 2016). The breeding season varies regionally but is strongly tied to monsoonal water levels, typically occurring from August to January in North India and from November to March in the South. As a highly visible and culturally significant species, it is a vital component of the socio-ecological fabric of Kokkare-Bellur.

Black-crowned Night Heron (*Nycticorax nycticorax*)

A cosmopolitan species listed as Least Concern, the Black-crowned Night Heron is a medium-sized (66 cm), stocky waterbird with a global distribution. As its name suggests, it is primarily nocturnal or crepuscular, a temporal niche that helps it avoid competition with diurnal herons and egrets. It feeds on a wide and generalist diet of fish, insects, amphibians, and even small rodents (Hothem *et al.* 2020). It breeds in dense colonies throughout India, often in the inner, more concealed portions of mixed-species heronry trees, utilizing a range of wetland habitats from freshwater marshes to estuarine mangroves (Narayanan and Vijayan, 2007). The breeding season is highly variable across its range, often linked to local rainy seasons, with peaks observed from March to August in northern India and during both monsoons in the south (Sashikumar *et al.* 2011). Its presence at Kokkare-Bellur adds a significant dimension to the

study of niche partitioning, particularly in its temporal and fine-scale spatial segregation from the larger, diurnal species.

Little Egret (*Egretta garzetta*)

This widespread, elegant, and highly adaptable small heron (65 cm) is listed as Least Concern due to its large global population. The Little Egret is an active and versatile visual hunter, employing a variety of techniques including stalking, running, and foot-stirring to catch its prey, which includes small fish, amphibians, crustaceans, and aquatic insects. It thrives in a broad spectrum of shallow water habitats, from small village ponds and irrigation canals to vast flooded fields and coastal mudflats. It breeds colonially throughout the Indian subcontinent, often in large mixed-species assemblages with other small herons and cormorants (Hilaluddin *et al.* 2003). The breeding season typically coincides with the monsoon, spanning from June to August in the north and occurring during the wetter months in the south (Gopi and Pandav, 2011). Its inclusion in this study allows for a critical examination of how smaller, more generalized species partition resources and coexist with larger, more specialized nesters within the same highly competitive colony structure.

Little Cormorant (*Microcarbo niger*)

The smallest (55 cm) of the focal species in this study, the Little Cormorant is a common and widespread pursuit-diving piscivore. It is listed as Least Concern and is known for its remarkable adaptability, inhabiting nearly any form of inland water body, from small ditches to large reservoirs. It feeds almost exclusively on small fish, which it expertly pursues and catches underwater (Chatterjee *et al.* 2024). Breeding occurs throughout the year across India, with pronounced peaks that correspond to local wet seasons and associated increases in fish availability. Its distinct foraging method (pursuit-diving vs. wading/surface-feeding) and its

small body size make it an ideal subject for studying the lower strata of vertical nest partitioning and its unique response to interspecific competition and environmental variables (Chatterjee *et al.* 2024).

Together, this ecologically diverse assemblage of five species provides a robust and comprehensive framework for investigating the core themes of this thesis. The significant gradient in body size allows for a direct and powerful test of the 'nesting height-body size hypothesis' of resource partitioning. The varied breeding and foraging behavior, enable a detailed analysis of how different resource dependencies influence breeding strategies, phenology, and responses to environmental change. Finally, the inclusion of both a globally threatened flagship species and several common, widespread species underscore the broad relevance of this research for both targeted species conservation and community-level ecosystem management in human-dominated landscapes.

1.5 Research Gaps, Thesis Rationale, and Outline

While the ecology of colonial waterbirds has been the subject of extensive global research, significant and critical knowledge gaps persist, particularly concerning the dynamics of multi-species assemblages in the unique socio-ecological contexts of tropical, human-dominated landscapes. The majority of existing studies have either focused on a single species, which inherently limits insights into community-level processes like interspecific competition and niche partitioning, or have been conducted in pristine, protected environments, which may not accurately reflect the complex suite of pressures and opportunities faced by the majority of waterbird populations in modern South Asia. This doctoral thesis is designed to directly address these gaps through an integrated, multi-chapter investigation at the unique natural and social

laboratory of Kokkare-Bellur. It aims to systematically dissect the key ecological drivers of population dynamics and reproductive success, moving logically from broad-scale climatic influences to fine-scale nest-site and individual-level decisions, and culminates in a synthesis of applied conservation and management actions that have been derived directly from the research findings.

The rationale for this thesis is built upon four interconnected research objectives; each designed to fill a specific knowledge gap and construct a cohesive scientific narrative. The first major gap lies in our quantitative understanding of how climatic variability, specifically monsoonal rainfall, drives breeding phenology across a community of waterbirds. While the link is qualitatively accepted, detailed, long-term, multi-species data are scarce. **Objective 1 (Chapter 3)** therefore seeks to decipher the precise role of rainfall on the nesting chronology and success of the five focal species. It asks how inter-annual variability in rainfall influences the initiation, duration, and success of nesting, and whether these responses are uniform or species-specific, reflecting different ecological strategies. This temporal analysis forms the foundational environmental framework for the entire thesis. The second gap concerns the mechanisms of coexistence in spatially constrained, human-modified heronries. While niche partitioning is a classic ecological concept, its specific manifestation in a village-based colony with a limited and unique suite of available nesting trees is poorly understood. **Objective 2 (Chapter 4)** addresses this by exploring nesting niche partitioning and sharing. It asks how these sympatric species partition critical nesting resources, examining both horizontal (spatial clustering, tree preference) and vertical (nest height stratification) dimensions to mitigate competition. This chapter moves from the temporal axis of the study to the spatial, elucidating the structural organization of the breeding community. The third critical gap is the lack of a synthetic understanding of the determinants of reproductive success. Nest survival is the ultimate metric of fitness, integrating the cumulative effects of all environmental, social, and

individual factors, yet few studies have modeled these complex interactions simultaneously for a multi-species assemblage in an anthropogenic landscape. **Objective 3 (Chapter 5)** aims to fill this gap by investigating the ecological dynamics influencing nest survival. It asks what the key temporal, climatic, social, and landscape-scale drivers of nest survival are for each species, explicitly testing hypotheses related to coloniality benefits and the "human shield" effect. This chapter synthesizes the temporal and spatial findings of the preceding chapters into a powerful, predictive model of reproductive outcomes. Finally, a significant gap exists between colony-based ecological studies and the landscape-level requirements of wide-ranging species, particularly concerning the post-release ecology of rehabilitated individuals. **Objective 4 (Chapter 6)** addresses this by mapping the foraging habitat dynamics and ranging patterns of the flagship Spot-billed Pelican. Using GPS telemetry on rescued individuals, it asks what the key foraging habitats are and how movement patterns differ between life-history stages and seasons. This expands the thesis's spatial scale from the colony to the landscape, providing crucial data for connectivity conservation and evaluating the success of rehabilitation interventions.

The structure of this thesis is designed to build a cohesive and compelling scientific narrative, where each research chapter addresses one of these core objectives, logically building upon the insights of the previous one and contributing to a holistic understanding of the system. Chapter 2 first provides a detailed description of the Study Area, establishing the unique geographical, ecological, and socio-cultural context of the Kokkare-Bellur Community Reserve. The thesis then sequentially presents the primary research findings. Chapter 3 examines the overarching influence of rainfall on breeding phenology. Chapter 4 investigates the spatial mechanisms of coexistence through niche partitioning. Chapter 5 synthesizes these factors to model the determinants of nest survival. Chapter 6 expands the spatial scope to explore the landscape-level movement ecology of the flagship pelican. Finally, Chapter 7 closes the research-to-

action loop by detailing the Conservation and Management outcomes derived from this doctoral work, demonstrating how the scientific knowledge generated in Chapters 3 through 6 has been translated into tangible, on-the-ground conservation strategies at KBCR. Through this logical progression from broad context to specific research questions and finally to applied outcomes, this thesis aims to make a significant and cohesive contribution to the fields of avian ecology, conservation biology, and the study of human-wildlife interactions in the Anthropocene.

Chapter – 2

STUDY AREA

2.1 Location

This study was conducted in the Kokkare-Bellur Community Reserve (KBCR), situated in Maddur Taluk, Mandya District, Karnataka, Southern India (12°13'N and 77°05'E). Spanning an area of approximately 3.12 square kilometers, this reserve is a unique example of an inland, mixed-species heronry nestled entirely within a living human settlement. The village lies to the west of the Shimsha River, and the surrounding landscape is a mosaic of paddy fields, sugarcane plantations, dryland crops, scattered tree groves, and numerous tanks and canals, which support critical foraging for colonial waterbirds (Fig. 2.1).

The reserve was officially notified as a Community Reserve in 2007, under Section 36C of the Wildlife (Protection) Act, 1972, recognizing the long-standing cultural coexistence between the human population and breeding birds. The area is devoid of a direct wetland source within the village boundary, making it the only known pelicanry in India where colonial waterbirds breed entirely within village limits, depending on external waterbodies for foraging.

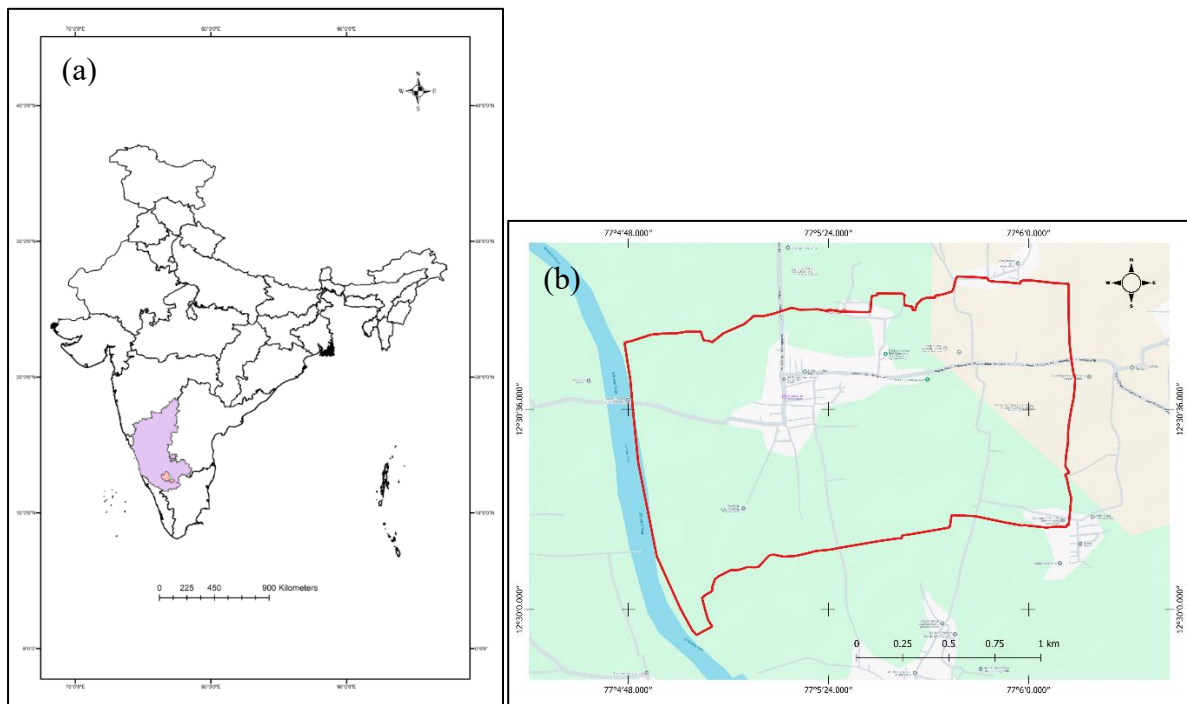
2.2 Physical Features

The terrain of Kokkare-Bellur is composed of gently undulating land interspersed with both irrigated and dry agricultural plots. The red loamy soils of the region are fertile and support a wide range of crops including paddy, sugarcane, coconut, and finger millet, along with other dryland crops such as groundnut, field beans, sesame, and turmeric (Manu and Jolly, 2000).

The region experiences a tropical climate, with a mean annual temperature of 25.3°C. Winters (December–February) are relatively mild, with temperatures ranging between 16–18°C, while the summer months (March–May) witness highs of 30–34°C. Rainfall is variable, averaging

750 ± 207 mm annually, with the Southwest Monsoon (June–September) contributing the bulk, and the Northeast Monsoon (October–December) providing an additional 20% (Shilpashree *et al.* 2016).

These climatic parameters, particularly rainfall onset and intensity, are closely linked to nest initiation, success, and chick survival, which were key parameters examined in this study.



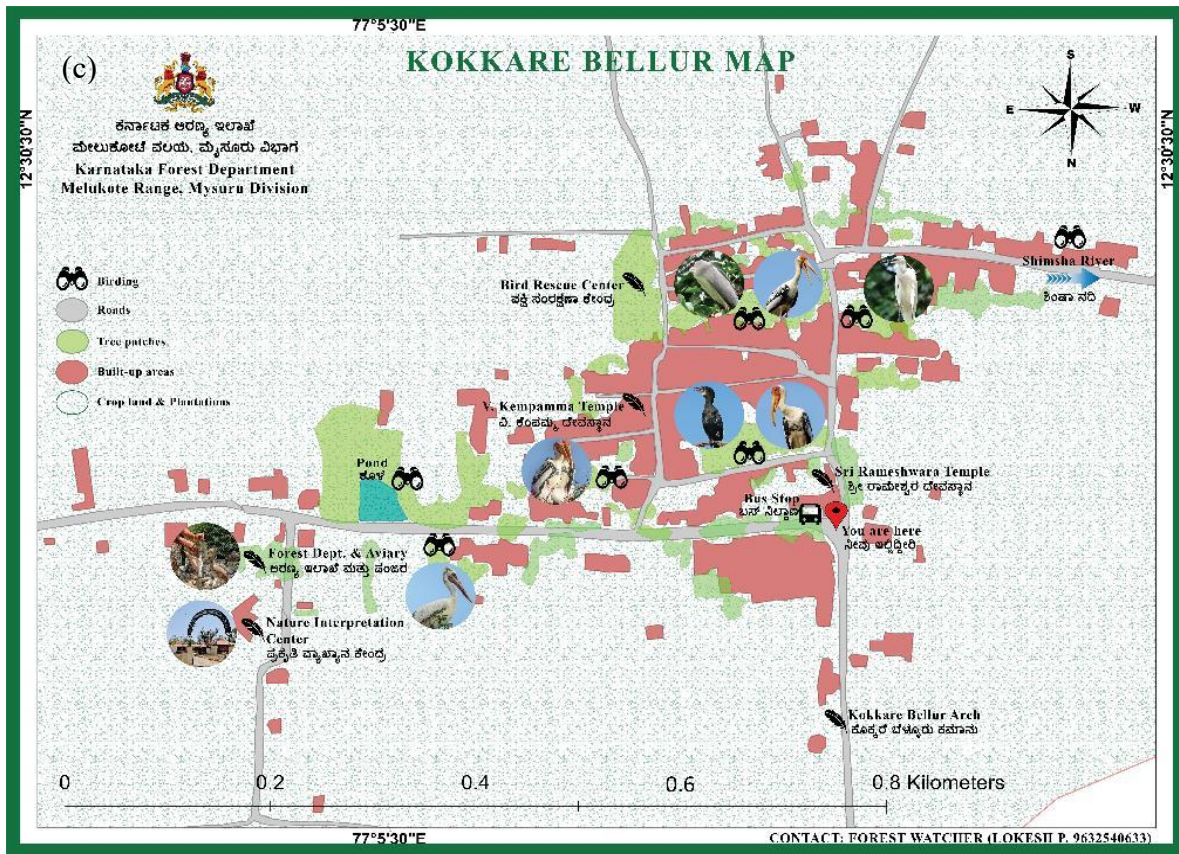


Figure 2.1. (a) Kokkare-Bellur, situated in southern Karnataka in peninsular India, (b) Village boundary bounded by Shimsha River from the west, and (c) Centre region of the village and tree patches used for nesting by the waterbirds.

2.3 Ecological Features

The nesting landscape in Kokkare-Bellur is composed of mature trees growing in backyards, roadsides, school premises, temple compounds, and agricultural bunds (Fig. 2.1, (c)). The primary tree species used for nesting include Tamarind (*Tamarindus indica*), Banyan (*Ficus benghalensis*), Peepal (*Ficus religiosa*), Portia (*Thespesia populnea*), White Gul Mohur (*Delonix elata*), Neem (*Azadirachta indica*), Monkey Pod (*Samanea saman*), *Melia dubia*, *Albizia lebbeck*, *Albizia amara*, and *Pongamia pinnata* are used opportunistically by all five nesting species (Manu and Jolly, 2000).

These trees serve not only as nesting platforms but also play a role in temperature regulation, protection from wind and predators, and canopy connectivity, which influences nest placement. Over time, many of these trees have become multi-generational nesting sites, with villagers protecting them from felling or lopping.

However, in recent years, several trees have been cut down for infrastructure expansion, including new houses, shops, and widened village roads. The loss of large, old nesting trees threatens the continuity of the heronry, especially for species that exhibit site fidelity and communal nesting (Subramanya, 1996; Manu and Jolly, 2000).

2.4 Kokkare-Bellur Mixed Heronry

Kokkare-Bellur is one of the oldest documented inland heronries in India, with early references by T.C. Jerdon from 1864 (Jerdon, 1971) and later formalized through conservation efforts by Neginhal (1977). The heronry derives its name from the Painted Stork, locally called “Kokkare” in Kannada, symbolizing the cultural and ecological identity of the village.

Five main species of colonial waterbirds nest within this village landscape: the Spot-billed Pelican (*Pelecanus philippensis*), listed as Near Threatened, the Painted Stork (*Mycteria leucocephala*), now listed as Least Concern, along with three smaller waterbird species, Black-crowned Night Heron (*Nycticorax nycticorax*), Little Cormorant (*Microcarbo niger*), and Little Egret (*Egretta garzetta*), all of which are classified as Least Concern.

The Spot-billed Pelican and Painted Stork dominate the upper canopies of mature trees, while the smaller species often utilize the inner branches and lower crowns of the same trees or nearby vegetation. This vertical and spatial segregation allows for niche partitioning within a compact nesting space, a phenomenon extensively studied during this research.

The Spot-billed Pelican, being an obligate piscivore, depends on external lakes and deep tanks for feeding, while the Painted Stork and other smaller waterbirds use a variety of shallow

wetlands, rice paddies, irrigation channels, and flooded fields to forage on small fish, amphibians, crustaceans, reptiles, and insects.

2.5 Social and Cultural Value

Kokkare-Bellur is globally acclaimed for its intimate human-bird relationship, considered a rare example of community-led coexistence. Birds are regarded with reverence and emotional attachment, often referred to as "daughters of the village" who return each year to give birth and raise young.

Villagers traditionally rescue fallen chicks, providing them shelter and care, and in return, they benefit from the nutrient-rich guano, which was once widely used as natural fertilizer (Subramanya, 1996; Manu and Jolly, 2000). This mutualistic relationship has allowed colonial waterbirds to thrive for decades within this human-dominated landscape.

However, rapid urbanization, modern lifestyles, and changing aspirations have begun to alter this dynamic. Increasing demands for land, privacy, and aesthetic modification have resulted in a decline in traditional tree protection, and in some cases, villagers have sought official permission to remove nesting trees near their homes (Manu and Jolly, 2000).

Despite these pressures, the cultural ethos of Kokkare-Bellur continues to support the conservation narrative, and community sensitization, education, and compensatory incentives have emerged as crucial strategies for ensuring the continued survival of this unique heronry.

2.6 Avifaunal Research and Monitoring

Scientific interest in Kokkare-Bellur has evolved over the last few decades. Although early reports of pelican presence date back to the 19th century, systematic ornithological studies began in the late 20th century. Notable research by Kannan and Manakadan (2005) and Kannan and Pandiyan (2012) estimated the Spot-billed Pelican nesting population to range between

134 and 544 individuals, with a mean value of 288.75 ± 142.11 nests over various years. A single historical record by T.C. Jerdon from the 1960s cited 2000 individuals, though it lacks verification and is considered anecdotal.

Most previous assessments were single-day counts conducted at non-standardized times during the breeding season, thus offering only a crude understanding of true population dynamics.

The present study, initiated in November 2018 by the Karnataka Forest Department, was designed to address this gap by implementing a long-term, season-wide monitoring framework. The objectives included: establishing baseline nesting data, investigating species-specific mortality patterns, and examining whether parasitic nematode infestations, notably recorded in 2015–2018, were impacting pelican health and survival (Kumar *et al.* 2018).

Additionally, this research evaluated nest site preferences, nest survival factors, interspecific spacing, tree patch dynamics, and foraging ranges, themes that have significant implications for management.

2.7 Conservation Significance

Kokkare-Bellur holds immense conservation importance as a model of community-based bird conservation, a functional Important Bird Area (IBA), and one of the few remaining inland pelicanries in India (Subramanya, 1996). Its ecological uniqueness is matched by its cultural value, making it a biodiversity and heritage hotspot.

Yet, the heronry now faces multiple threats such as loss of nesting trees, habitat degradation, declining community engagement, wetland pollution, and periodic mortality events linked to parasitism or disease (Manu and Jolly, 2000; Kumar *et al.* 2018). These underscore the urgent need for integrated conservation actions that combine ecological restoration, community participation, and sustained scientific monitoring.

The insights derived from this research provide a critical foundation for science-based habitat management, policy formulation, and future ecological studies across similar landscapes in India.

Chapter – 3

Deciphering the role of rainfall on nesting chronology at Kokkare-Bellur, Southern India, a multi-species colonial nesting waterbird site

3.1 Introduction

Colonial waterbirds represent some of the most ecologically informative components of wetland ecosystems, owing to their high trophic position, strong dependence on aquatic productivity, and sensitivity to environmental change. Their presence, abundance, and reproductive output are widely recognized as robust indicators of wetland health and ecosystem integrity (Amat and Green, 2009). Approximately one in eight bird species globally adopts a colonial breeding strategy (Rolland *et al.* 1998), forming dense aggregations that include herons, egrets, storks, pelicans, cormorants, ibises, and spoonbills. These colonies, variously termed heronries, rookeries, or pelicanries, function as dynamic ecological hubs, where breeding success emerges from a complex interplay of climatic conditions, resource availability, interspecific interactions, and anthropogenic pressures (Subramanya, 1996; Urfi, 2011).

The timing of breeding, or nesting chronology, is a central axis along which these interactions are structured. Nesting chronology encompasses the initiation, progression, and completion of reproductive events, including nest construction, egg laying, incubation, hatching, and fledging. For colonial waterbirds, the synchronization of these stages with favorable environmental conditions is critical, as the energetic demands of egg production and chick provisioning are exceptionally high. Consequently, even modest deviations from optimal timing can result in reduced reproductive success and compromised recruitment (Newton, 2010).

Across latitudinal gradients, the environmental cues governing nesting chronology differ markedly. In temperate regions, predictable changes in photoperiod and temperature reliably regulate breeding schedules (Crick, 2004). In contrast, in tropical and subtropical systems, particularly across South Asia, seasonal rainfall emerges as the dominant driver of ecosystem productivity and biological timing (Stutchbury and Morton, 2001). In the Indian subcontinent, the Southwest and Northeast monsoons govern wetland hydrology by replenishing rivers, filling irrigation tanks, and inundating agricultural landscapes. This monsoonal pulse directly determines the abundance and accessibility of aquatic prey such as fish, amphibians, and macroinvertebrates, which form the primary food base for most colonial waterbirds (Frederick and Loftus, 1993).

For waterbirds, rainfall therefore acts as both a proximate cue and an ultimate driver of breeding. Periods of adequate and well-timed rainfall enhance habitat suitability, stabilize water levels, and support prey populations, enabling birds to initiate nesting earlier and sustain prolonged breeding seasons. Conversely, delayed, insufficient, or erratic rainfall can reduce food availability, increase foraging distances, and expose nests to heightened risks of failure. Climate-driven alterations in rainfall regimes have been shown to generate phenological mismatches between breeding demand and prey availability, leading to reduced chick survival and population declines (Both *et al.* 2006; Visser *et al.* 2006; Spalding *et al.* 2010).

These risks are magnified in colonial systems, where large numbers of individuals breed simultaneously in spatially constrained habitats. While coloniality offers well-documented benefits, including enhanced predator detection, communal defense, and improved foraging efficiency through information transfer (Ward and Zahavi, 1973; Wittenberger and Hunt, 1985; Danchin and Wagner, 1997), it also intensifies competition for nesting sites and food resources. As a result, rainfall-driven fluctuations in resource availability can have disproportionate

effects on nesting success, particularly in mixed-species colonies where species differ in body size, foraging mode, and energetic requirements (Burger, 1979; Brown and Brown, 2001).

In India, these dynamics unfold within a distinctive socio-ecological context. Unlike many temperate systems, a large proportion of Indian heronries are embedded within human-dominated agricultural and village landscapes rather than remote protected areas (Subramanya, 1996; Urfi, 2011). While such proximity exposes birds to threats such as habitat loss, pollution, and disturbance (Manakadan and Kannan, 2003; Sundar, 2004), it can also generate unique conservation outcomes. Long-standing cultural tolerance and protection have allowed several major heronries to persist for centuries, sometimes benefiting from a “human shield” effect that deters natural predators (Tryjanowski *et al.* 2013; Abbasi and Khan, 2023). Within these systems, rainfall assumes heightened importance, as breeding success depends not only on climatic conditions but also on the capacity of birds to exploit human-modified wetlands whose productivity is tightly coupled with monsoonal variability.

Kokkare–Bellur Community Reserve (KBCR) exemplifies this complex interaction between climate, ecology, and society. Situated in the semi-arid rain-shadow region of southern India, KBCR supports a long-established, mixed-species colonial waterbird assemblage nesting entirely within a living village landscape. The site lacks a large permanent wetland; instead, breeding birds rely on a dispersed network of seasonal resources, including the Shimsha River, irrigation tanks, and flooded agricultural fields. In such a system, the timing, intensity, and duration of monsoonal rainfall are expected to exert strong control over food availability, breeding initiation, nesting duration, and reproductive success.

Despite the ecological significance of heronries such as Kokkare–Bellur, quantitative, multi-species assessments of how rainfall shapes nesting chronology in Indian colonial waterbirds remain scarce. Existing studies have largely focused on single species, short temporal scales, or protected wetland systems, limiting broader inference across diverse breeding assemblages

and human-dominated landscapes (Urfi, 2011; Tiwary and Urfi, 2016). There is a critical need for long-term, community-level analyses that explicitly link rainfall variability to nesting phenology and breeding outcomes across coexisting species with differing ecological strategies.

This chapter addresses this gap by examining the role of rainfall in structuring nesting chronology and reproductive success among colonial waterbirds at Kokkare–Bellur. By analyzing inter-annual variation in rainfall alongside systematic nesting data, this study evaluates how climatic variability influences the initiation, duration, and success of breeding across multiple species within a shared socio-ecological landscape. It establishes the temporal framework upon which subsequent chapters build, providing essential context for understanding spatial niche partitioning, nest survival dynamics, and landscape-level movement ecology. In doing so, this chapter contributes to a deeper understanding of how climate variability, particularly monsoonal rainfall, shapes the reproductive ecology of colonial waterbirds in the Anthropocene and informs conservation strategies for heronries embedded within human-dominated environments.

Research Objectives and Hypotheses:

Research Objective: The primary objective of this study is to investigate the influence of rainfall patterns on nesting chronology and reproductive success among colonial waterbirds at Kokkare-Bellur, Southern India.

- a) How does rainfall influence the initiation and duration of nesting activities across different waterbird species at Kokkare-Bellur?
- b) To what extent do rainfall patterns influence the nesting success and failures among different waterbird species?

Hypothesis: Variations in rainfall patterns will significantly affect the timing and success of nesting activities among colonial waterbirds at Kokkare-Bellur. Specifically, periods of increased rainfall will coincide with earlier onset and peak breeding events, as well as higher reproductive success rates, due to enhanced food availability and habitat quality. Conversely, reduced rainfall will lead to delayed nesting activities, decreased breeding success, and potentially lower fledgling survival rates, as resources become limited and environmental stressors intensify. Testing these hypotheses aims to elucidate the role of rainfall in shaping nesting chronology and reproductive outcomes among colonial waterbirds, thereby contributing to understanding avian ecology and informing conservation management strategies in the face of changing climatic conditions.

3.2 Methods

Data collection

The heronry censuses were conducted from October 2018 to September 2023 across five breeding seasons. To determine the arrival date of birds and nest monitoring in the heronry, we carried out systematic surveys every alternate day. We collected information on the number of active nests, and eventually, towards the end of nesting season, the number of successful nests and number of chicks fledged per nest. Nests were considered active only when we confirmed incubation began and nests were considered as successful when at least one young fledged successfully. Nesting duration was calculated for each nest as the total number of days, starting when the adults began incubation to the date the last young fledged successfully. Censuses were conducted on the ground by visiting each nesting tree and monitoring the individuals and nests using binoculars (Nikon Aculon A211, 10-22 × 50X). Nest maps were created for each

tree to uniquely identify each nest of different waterbird species and numbers to each nest were given based on the first arrival to the given tree. Rainfall data were collected from the Karnataka State Natural Disaster Monitoring Centre for the nearest Rain Gauge Station situated at Maddur Taluk from January 2018 to September 2023.

Data Analysis

The analysis was structured around the creation of a multi-panel graph to elucidate the relationship between monsoon trends and nesting patterns across the five breeding seasons. This graphical representation aimed to identify correlations between rainfall intensity and duration with the initiation and success rates of nesting activities among different waterbird species. Statistical analyses were conducted to quantify these relationships, providing a comprehensive understanding of the impact of rainfall on the nesting chronology at Kokkare-Bellur. Poisson regression analysis assessed significant differences in nesting duration across breeding seasons and species (Zuur *et al.* 2010). Pearson chi-square tests examined nesting success variation among waterbirds across the breeding season (Agresti and Kateri, 2025). Fisher's Exact Test analyzed nesting success variation of smaller waterbirds across multiple nesting events during different breeding seasons (McDonald, 2014). Poisson regression coefficients (vglm) for nesting duration were calculated for different waterbird species across the nesting seasons (Yee, 2015).

3.3 Results

We observed substantial variation in rainfall patterns across different years. Notably, 2018 stood out from the other years as it exhibited a distinct single peak in rainfall during May, reaching a maximum of 302 mm. In contrast, the remaining years displayed a multi-peaked distribution of precipitation. The years 2019 through 2022 consistently recorded their

maximum precipitation during the period extending from September to November. Furthermore, the total precipitation accumulated throughout these years showed fluctuations, with high rainfall recorded in 2021, 2019, and 2020 and comparatively lower levels observed in 2018 and 2022 (Fig. 3.1).

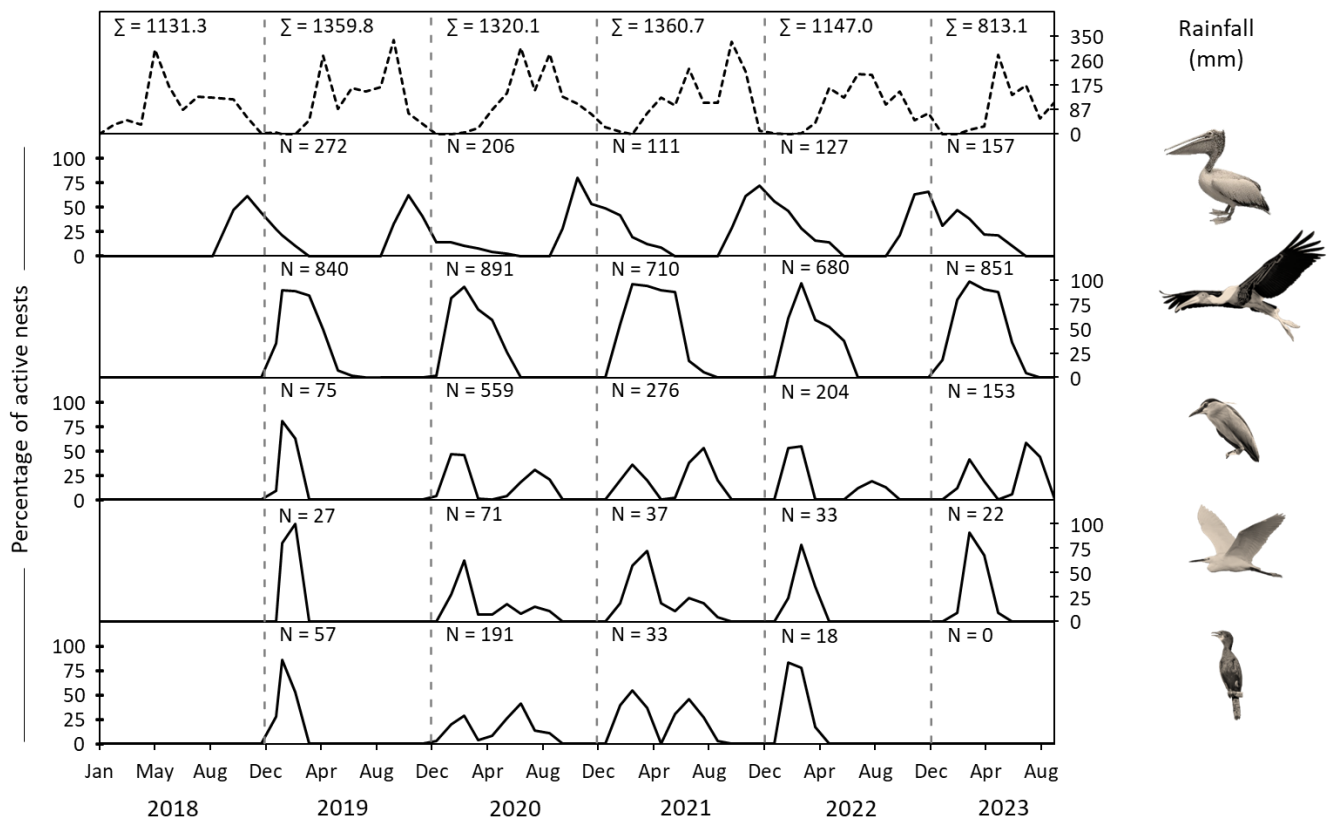


Figure 3.1. Nesting patterns of waterbirds (Spot-billed Pelican, Painted Stork, Black-crowned Night Heron, Little Egret, Little Cormorant: arranged in body size gradient from top to bottom) at Kokkare-bellur Community Reserve from October 2018 - September 2023. Σ value represents total rainfall in mm recorded in a particular year. N is the number of active nests for a specific breeding season.

In terms of nesting numbers the dominant species were the Painted Stork with more than 600 to 800 nests recorded in the area. The Storks across years commenced nesting from mid-January and completed nesting mostly by August. followed by the Black-crowned Night Heron. The number of nests of pelicans declined from 2018 to 2021, followed by an increase in the subsequent two seasons. While in the case of the smaller waterbird species (Black-crowned Night Heron, Little Egret and Little Cormorant) the number of nests increased drastically in 2020, followed by a continuous decline over the subsequent three seasons (Fig. 3.1).

Among the five waterbird species studied, the Spot-billed Pelican consistently initiated nesting in October, which was earlier than other species (Fig. 3.1). While all other species commenced nesting from January onwards. Painted Stork, for the most part, also consistently initiated nesting at the same time every year, except during the nesting season of 2020-21. However, in the case of the smaller waterbird species, there was a gradual delay in the commencement of nesting in each successive year (Fig. 3.1).

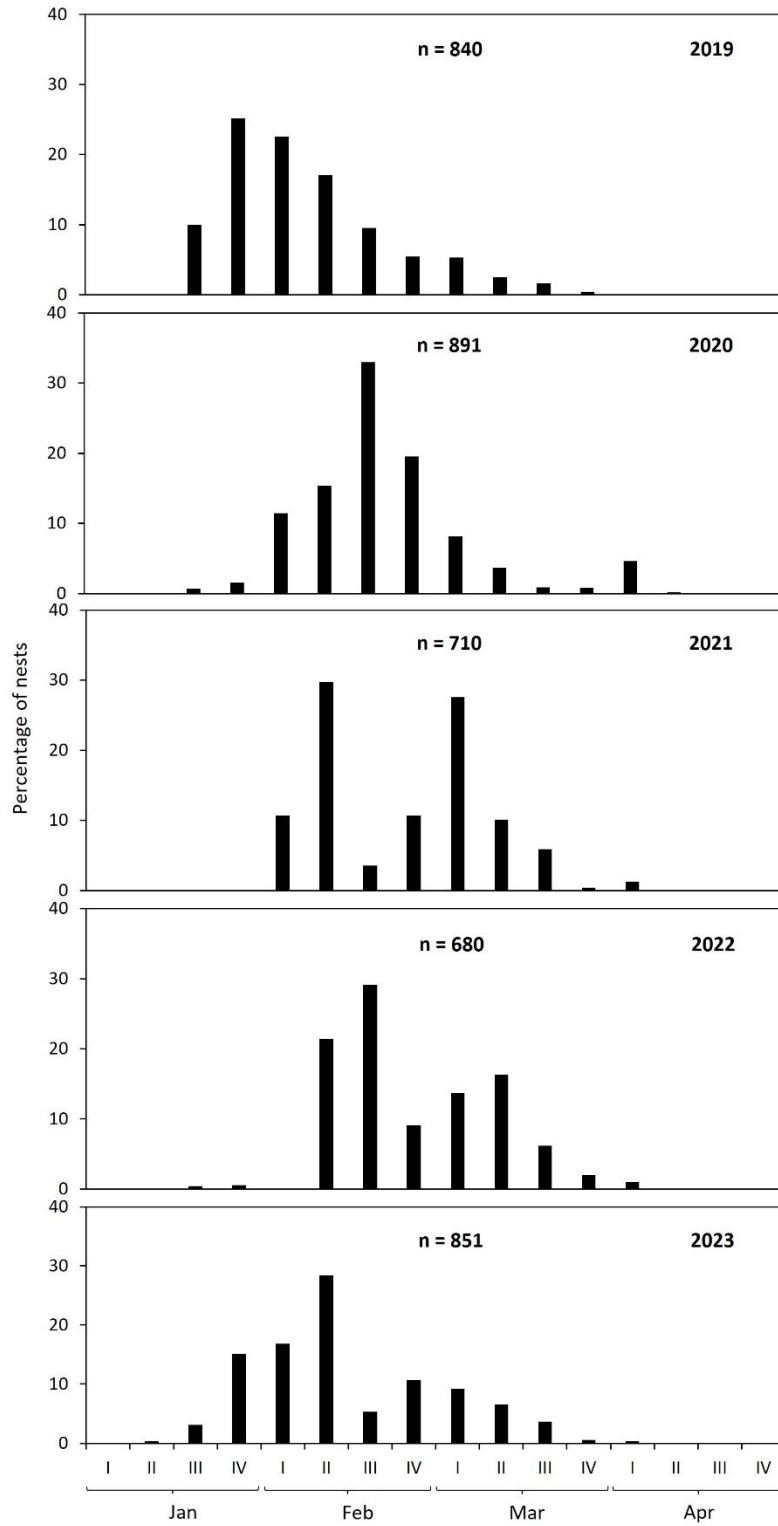


Figure 3.3. Variation in nest initiation dates of Painted Stork in Kokkare-Bellur during 2019-

23.

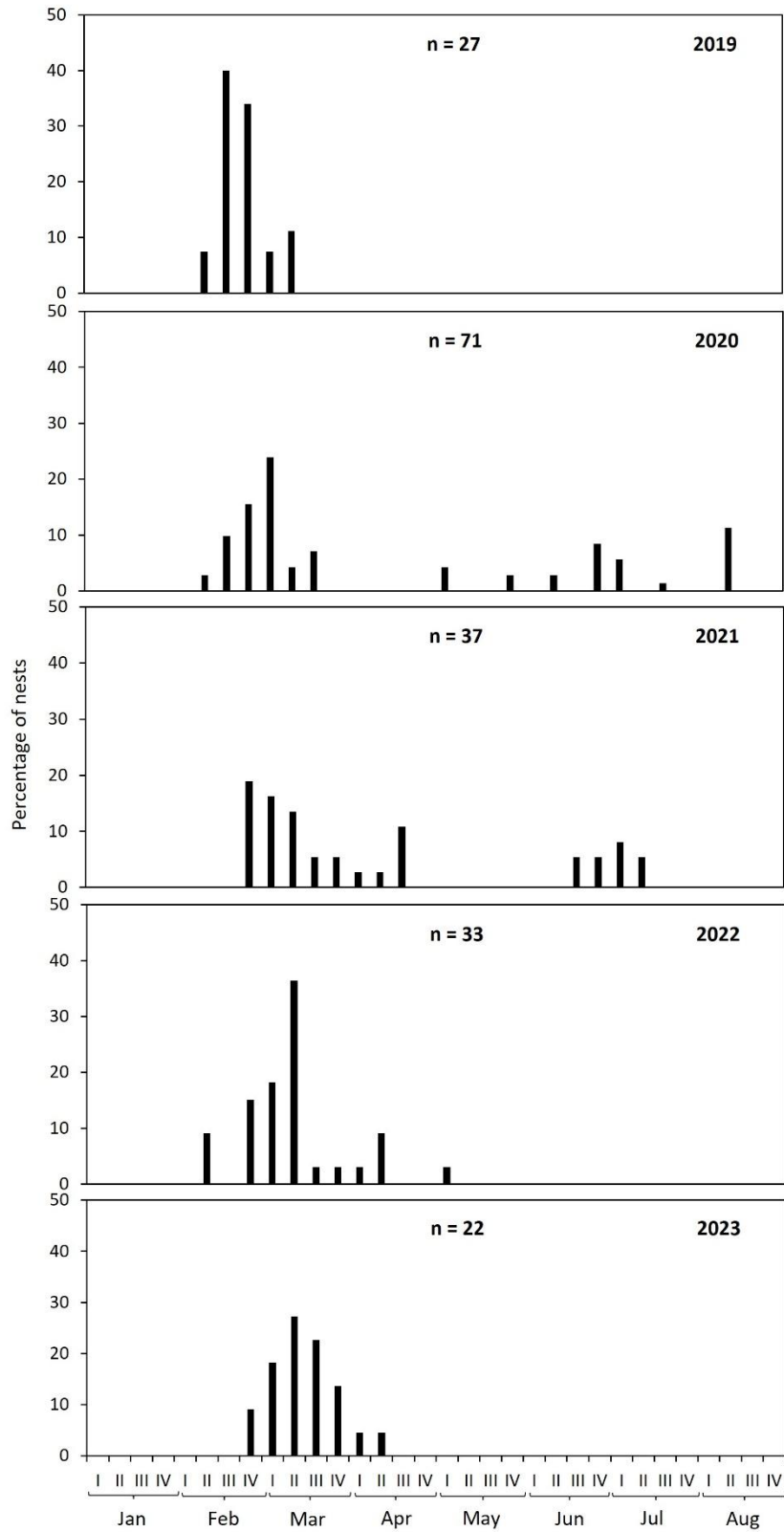


Figure 3.5. Variation in nest initiation dates of Little Egret in Kokkare-Bellur during 2019-

23.

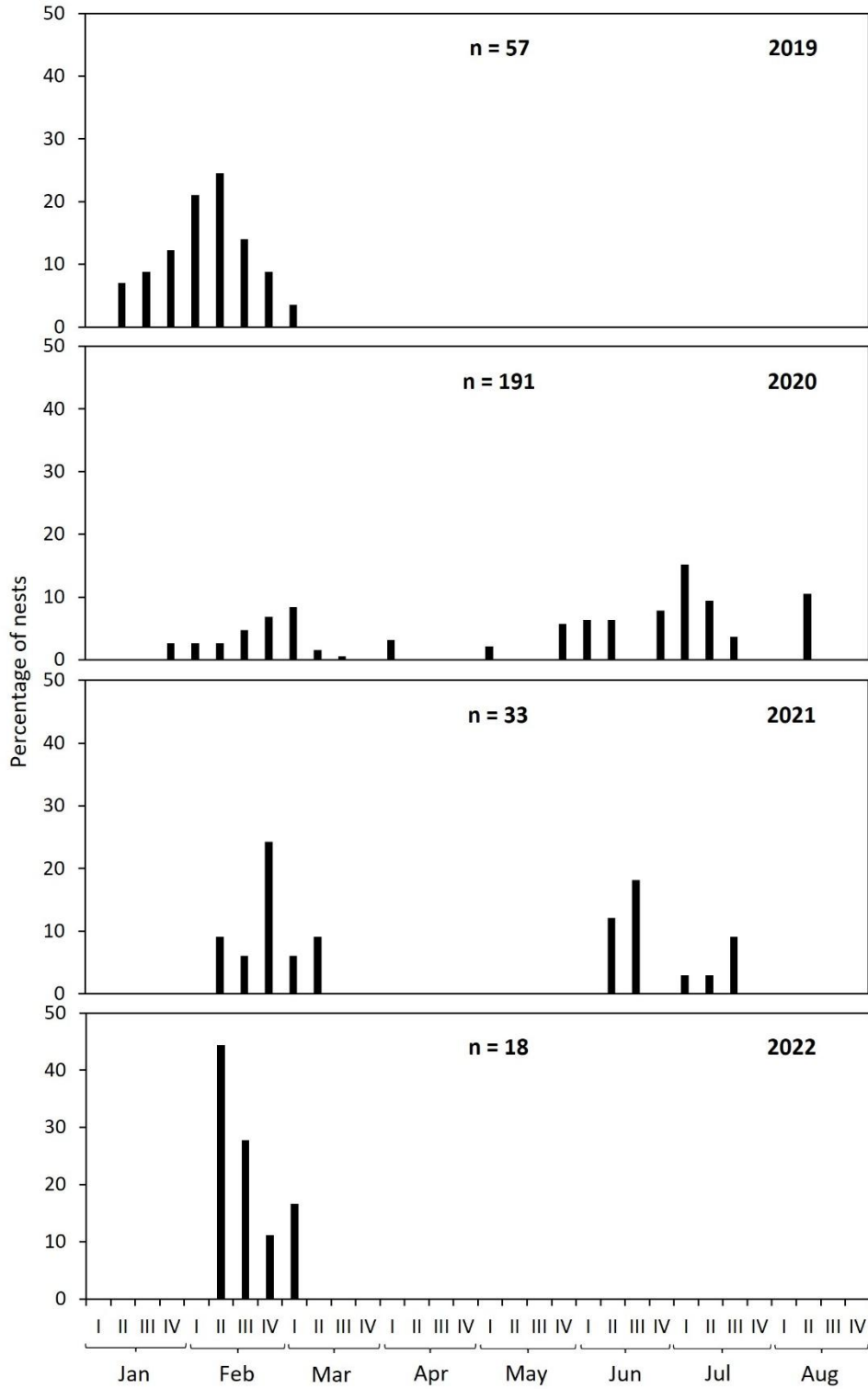


Figure 3.6. Variation in nest initiation dates of Little Cormorant in Kokkare-Bellur during 2019-23.

The two larger waterbird species displayed a unimodal nesting pattern, characterized by a breeding period lasting between 6 to 9 months. In contrast, the three smaller waterbird species exhibited a variation in their nesting patterns. All three exhibited a unimodal nesting pattern in the first year. After which, the Black-crowned Night Heron displayed a bimodal pattern for the subsequent four seasons. The Little Egret displayed two bimodal nesting patterns followed by two unimodal patterns. The Little Cormorant exhibited two bimodal patterns followed by a unimodal pattern and did not engage in nesting activities in 2023. The breeding period for the smaller waterbird species lasted for 2 to 3 months (Fig. 3.2 to Fig. 3.6).

Nesting duration of waterbirds

There was significant variation in the nesting duration for the waterbird species across the years except for the Spot-billed Pelican. In case of Spot-billed Pelican, only in the last season there was significant increase in the nesting duration i.e. an average of 140 days ($p < 0.05$). In case of other species, a significant increase in nesting duration was observed for the year 2020-21 which also corresponded to higher annual and prolonged rainfall that year. Painted Stork nested for an average of 148 days ($p < 0.05$), Night Heron nested for an average of 68 days ($p < 0.05$), Little Egret nested for an average of 69 days ($p < 0.05$), and Little Cormorant nested for an average of 71 days ($p < 0.05$) in the 2020-21 nesting season (Fig. 3.7) (Table 3.1).

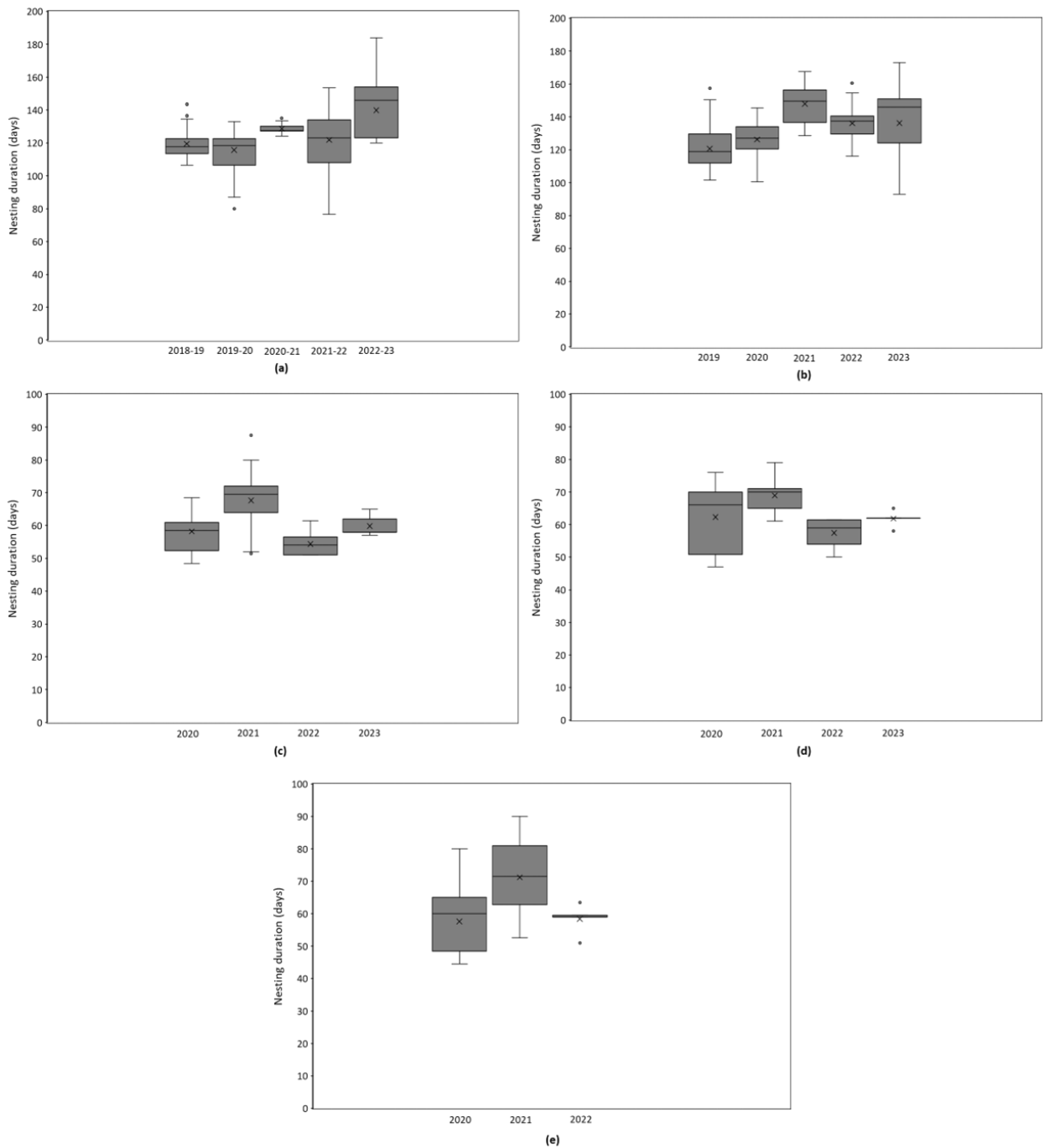


Figure 3.7. Box plot showing interannual variation of nesting duration for different waterbird species nesting at Kokkare-Bellur, (a) Spot-billed Pelican (b) Painted Stork (c) Black-crowned Night Heron (d) Little Egret (e) Little Cormorant. The thick horizontal stroke inside the box shows the median, the box represents the interquartile range, the vertical line extending from the box represents standard deviation. # For Night Heron,

Little Egret and Little Cormorant, data was not collected for the 2018-19 breeding season.

Table 3.1. Poisson regression coefficients for nesting duration for different waterbird species across the different nesting season. Year 1 = 2018-19 breeding season, Year 2 = 2019-20 breeding season, Year 3 = 2020-21 breeding season, Year 4 = 2021-22 breeding season, Year 5 = 2022-23 breeding season.

Species	Predictor variable	Coefficient (β)	Standard Error	Wald Chi-Square	p-value
Spot-billed Pelican	Year*Year1	0.059	0.066	0.888	0.374
	Year*Year2	0.025	0.067	0.379	0.704
	Year*Year3	0.101	0.067	1.507	0.131
	Year*Year4	0.075	0.067	1.115	0.265
	Year*Year5	0.213	0.067	3.169	<0.05
Painted Stork	Year*Year2	0.044	0.005	8.728	<0.05
	Year*Year3	0.204	0.004	42.572	<0.05

Species	Predictor variable	Coefficient (β)	Standard Error	Wald Chi-Square	p-value
	Year*Year4	0.118	0.005	19.870	<0.05
	Year*Year5	0.118	0.004	25.151	<0.05
Black-crowned Night Heron	Year*Year3	0.147	0.011	12.402	<0.05
	Year*Year4	-0.074	0.016	-4.652	<0.05
	Year*Year5	0.023	0.014	1.606	0.108
Little Egret	Year*Year3	0.098	0.031	3.181	<0.05
	Year*Year4	-0.083	0.039	-2.149	<0.05
	Year*Year5	-0.010	0.039	-0.256	0.797
Little Cormorant	Year*Year3	0.204	0.027	7.517	<0.05
	Year*Year4	-0.001	0.040	-0.040	0.968

Nesting success of waterbirds across different nesting season

Significant variations were observed in the proportion of successful nests among the various waterbird species across different breeding seasons. In all waterbird species, an interesting trend emerged: as the nesting population increased, the nesting success tended to decrease. This phenomenon was particularly evident in the case of the Spot-billed Pelican, where a notable 40% decline in nesting population was observed over a span of three years. During this period, the nesting success increased from 24% to 58% in the third breeding season.

In the case of the Painted Stork and the smaller waterbird species, a similar pattern emerged. During the second breeding season (2019-20), there was an increase in the nesting population, which coincided with a decline in nesting success. Also, during the fourth breeding season (2021-22), a significant decline in nesting success was recorded, compared to the other seasons. This decline can be attributed to the unusually high and extended rainfall observed during the last season, which likely had a substantial impact on breeding outcomes (Fig. 3.8) (Table 3.2).

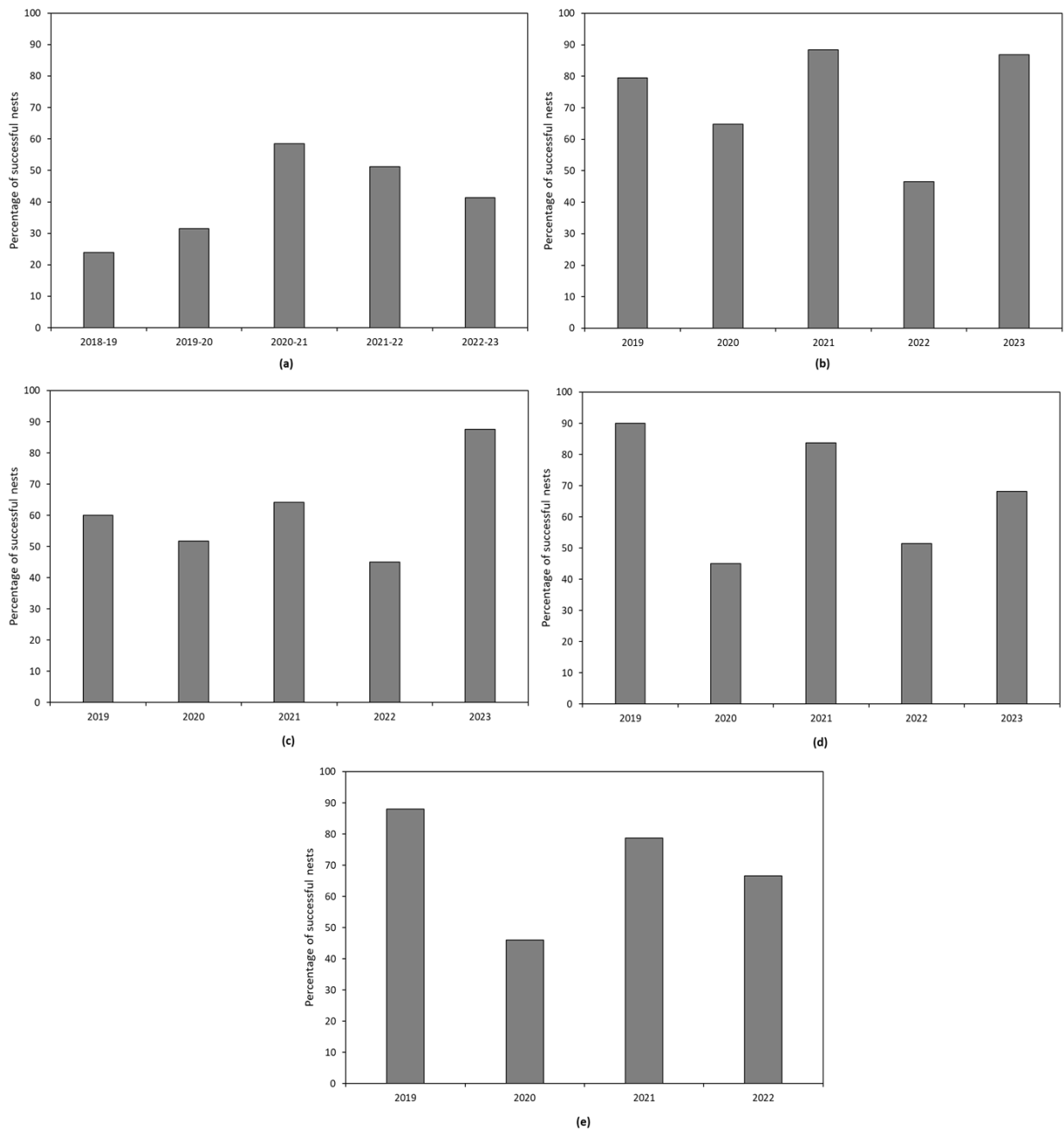


Figure 3.8. Inter-species variation in nesting success across the five breeding seasons for (a) Spot-billed Pelican (b) Painted Stork (c) Black-crowned Night Heron (d) Little Egret (e) Little Cormorant.

Table 3.2. Pearson Chi-Square values for nesting success variation of waterbirds across the breeding seasons.

Species	Pearson Chi-square (across years)	P value (df=4)
Spot-billed Pelican	55.604	<0.05
Painted Stork	467.24	<0.05
Black-crowned Night Heron	43.153	<0.05
Little Egret	31.184	<0.05
Little Cormorant	40.911	<0.05

Nesting success variation across multiple nesting events

In the case of the Black-crowned Night Heron, the second phase of nesting exhibited a significantly higher success rate, particularly during the years 2019-20 and 2020-21. In contrast, for the Little Cormorant, a significant decline in the success rate was observed during the second phase of nesting particularly in the year 2021-22. For the Little Egret, no significant association was found between the two nesting events across various seasons (Fig. 3.9 and Table 3.3).

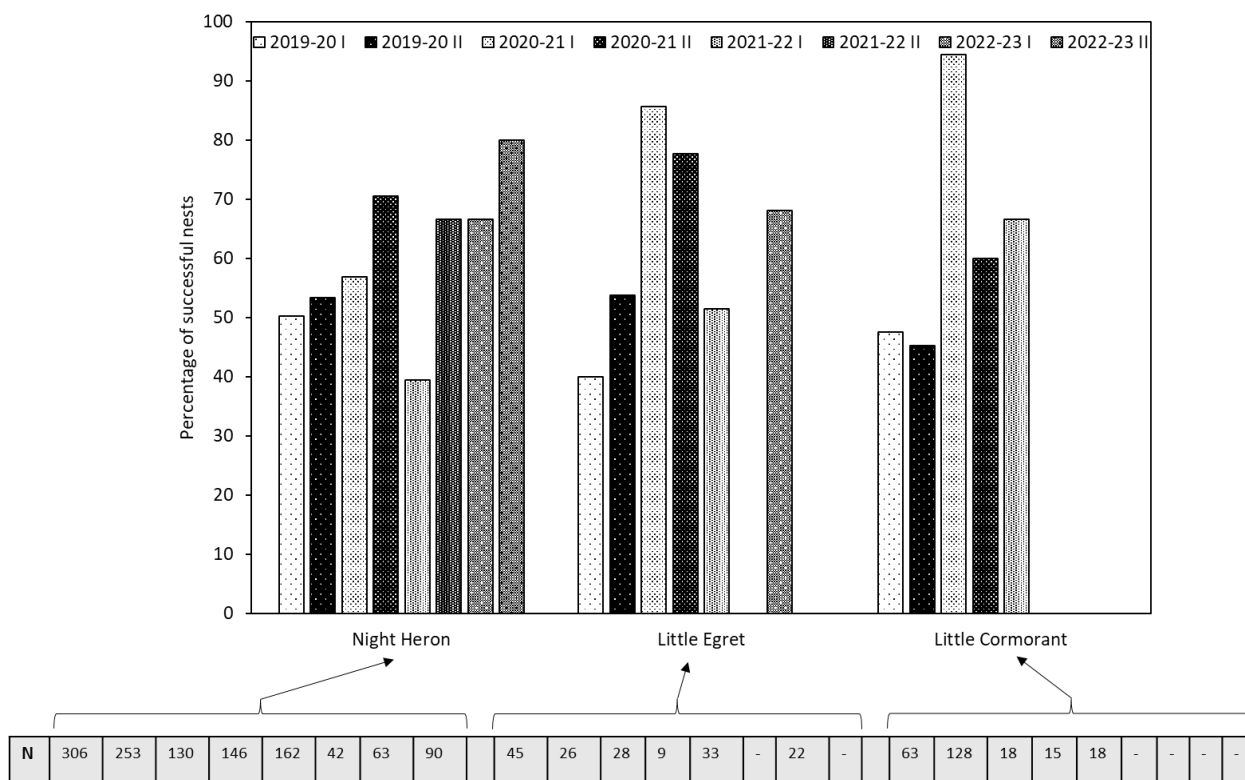


Figure 3.9. Inter-species variation in nesting success when there were multiple nesting events in a single nesting season. In the box below the value of N represents the total number of active nests during the multiple nesting events in a particular breeding season.

Table 3.3. Fisher’s Exact Test for nesting **success** variation of smaller waterbirds across the multiple nesting events during different breeding seasons.

Species	Comparison between multiple events	P value	95% Confidence Interval	Sample Estimates Odd Ratio
Black-crowned Night Heron	2019-20 A : 2019-20 B	0.497	0.797-1.598	1.128

Species	Comparison between multiple events	P value	95% Confidence Interval	Sample Estimates Odd Ratio
	2020-21 A : 2020-21 B	<0.05	1.070-3.074	1.808
	2021-22 A : 2021-22 B	<0.05	1.424-6.771	3.045
	2022-23 A : 2022-23 B	0.089	0.898-4.464	1.990
Little Egret	2019-20 A : 2019-20 B	0.324	0.591-5.194	1.736
	2020-21 A : 2020-21 B	0.619	0.066-7.848	0.592
Little Cormorant	2019-20 A : 2019-20 B	0.877	0.476-1.747	0.911
	2020-21 A : 2020-21 B	<0.05	0.002-1.124	0.111

Variation in chicks fledged per nest across the years

In terms of the number of chicks that successfully fledged from their nests, there were no significant differences observed across years for most waterbird species, except for the Spot-billed Pelican. In the case of Spot-billed Pelicans, despite an increasing trend in nesting success, there was a notable decrease in the number of chicks that successfully fledged over the years ($p < 0.05$) (Table 3.4). The mean number of chicks fledged per nest in this species decreased from 1.7 in the first season to 1.1 and 1.2 in the last two seasons, respectively (Fig. 3.10).

Painted Stork and Little Egret exhibited a higher mean number of chicks fledged per nest compared to other waterbird species, with a mean of 1.8 chicks fledged per nest and a maximum of 3 chicks observed in some cases. While, Little Cormorant had a mean number of 1.7 chicks fledged per nest, and Night Heron recorded a mean of 1.5 chicks per nest (Fig. 3.10).

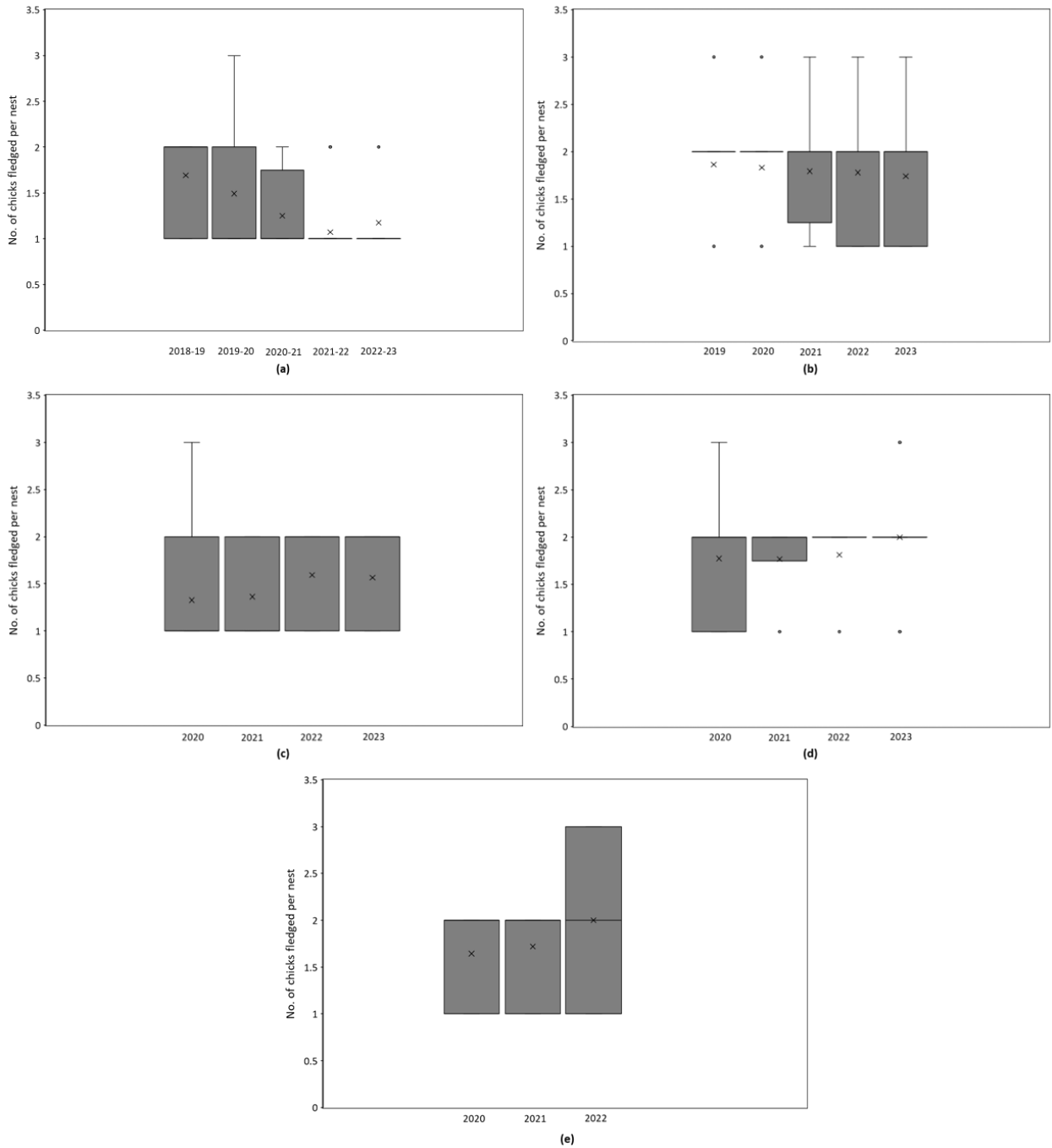


Figure 3.10. Box plot of inter-species variation in the number of chicks fledged per nest for (a) Spot-billed Pelican (b) Painted Storks (c) Black-crowned Night Heron (d) Little Egret € Little Cormorant, across the five breeding seasons. The thick horizontal stroke inside the box shows the median, the box represents the interquartile range, the vertical line extending from the box represents standard deviation. Data for Night Heron, Egret and Cormorant for 2018-19 season was not recorded.

Table 3.4. Poisson regression coefficients (vglm) for nesting duration for different waterbird species across the different nesting season. Year 1 = 2018-19 breeding season, Year 2 = 2019-20 breeding season, Year 3 = 2020-21 breeding season, Year 4 = 2021-22 breeding season, Year 5 = 2022-23 breeding season.

Species	Predictor variable	Coefficient (β)	Standard Error	Wald Chi-Square	p-value
Spot-billed Pelican	Year*Year2	-1.261e-01	1.417e-01	-0.890	0.3735
	Year*Year3	-3.029e-01	1.469e-01	-2.062	<0.05
	Year*Year4	-4.571e-01	1.605e-01	-2.848	<0.05
	Year*Year5	-3.643e-01	1.435e-01	-2.539	<0.05
Painted Stork	Year*Year2	-1.820e-02	4.184e-02	-0.435	0.664

Species	Predictor variable	Coefficient (β)	Standard Error	Wald Chi-Square	p-value
	Year*Year3	-3.960e-02	4.114e-02	-0.963	0.336
	Year*Year4	-4.704e-02	5.060e-02	-0.930	0.353
	Year*Year5	-6.939e-02	3.977e-02	-1.745	0.081
Black-crowned Night Heron	Year*Year3	2.857e-02	8.208e-02	0.348	0.727
	Year*Year4	1.844e-01	9.699e-02	1.902	0.057
	Year*Year5	1.614e-01	9.068e-02	1.780	0.075
Little Egret	Year*Year3	-3.969e-03	1.890e-01	-0.021	0.983
	Year*Year4	2.346e-02	2.232e-01	0.105	0.916
	Year*Year5	1.158e-01	2.256e-01	0.514	0.608
Little Cormorant	Year*Year3	4.917e-02	1.706e-01	0.288	0.773
	Year*Year4	1.938e-01	2.204e-01	0.879	0.379

3.4 Discussion

The present study demonstrates that rainfall acts as a primary ecological driver shaping nesting chronology, nesting duration, and reproductive outcomes of colonial waterbirds at Kokkare-Bellur. The pronounced inter-annual variability in rainfall patterns observed during the five-year study period provides strong evidence that monsoonal precipitation governs breeding phenology in tropical waterbird communities, primarily through its influence on wetland hydrology and prey availability (Frederick and Loftus, 1993; Stutchbury and Morton, 2001). In tropical systems where photoperiodic cues are weak, rainfall functions as both a proximate environmental signal and an ultimate determinant of breeding success, a pattern that has been widely documented across waterbird assemblages (Amat and Green, 2009; Newton, 2010).

The observed variation in nesting initiation dates and nesting durations among species reflects a high degree of behavioral plasticity in reproductive strategies. Such plasticity is widely recognized as an adaptive response that allows birds to cope with environmental unpredictability and temporal variability in resources (Drent and Daan, 1980; Visser *et al.* 2004). At Kokkare-Bellur, the ability of multiple species to adjust breeding schedules in accordance with rainfall patterns suggests a fine-tuned response to hydrological conditions that regulate food availability and nesting site suitability. Larger-bodied species such as the Spot-billed Pelican and Painted Stork exhibited predominantly unimodal nesting patterns, indicating relatively constrained breeding windows likely associated with greater energetic demands, longer chick-rearing periods, and reduced flexibility in breeding timing (Lack, 1968; Newton, 1998). In contrast, smaller species such as the Black-crowned Night Heron, Little Egret, and Little Cormorant frequently displayed bimodal nesting patterns, suggesting greater temporal flexibility and an enhanced ability to exploit multiple peaks in resource availability (Durant *et al.* 2007).

The strong positive relationship between rainfall intensity and nesting duration further highlights the central role of precipitation in shaping reproductive strategies. Years characterized by sustained or well-distributed rainfall supported extended nesting durations, particularly among larger species, indicating that prolonged food availability enables sustained breeding effort and may enhance chick survival (Both *et al.* 2006; Winkler *et al.* 2013). Conversely, fragmented or erratic rainfall regimes were associated with shortened nesting periods and reduced nesting success in some species, reflecting constraints imposed by limited or unstable prey resources. Such rainfall-mediated shifts in breeding phenology are consistent with broader evidence linking climate variability to phenological mismatches and reduced reproductive performance in birds (Crick, 2004; Visser *et al.* 2006).

Density-dependent processes emerged as an additional key factor influencing nesting success at the colony. The negative association between nesting population size and reproductive success across breeding seasons indicates that increasing colony density intensifies competition for limited resources, including food and suitable nesting substrates (Lack, 1954; Sutherland, 1996). This pattern was particularly pronounced in the Spot-billed Pelican, where increases in nesting population size over successive seasons coincided with declining nesting success, suggesting that local carrying capacity may be periodically exceeded during peak breeding years (Newton, 1998; Krebs, 2009). Heightened intra-specific competition and increased energetic demands during chick provisioning likely constrain reproductive output under high-density conditions. However, contrasting responses among co-nesting species indicate that density dependence operates in a species-specific manner, influenced by differences in foraging range, diet breadth, and nesting microhabitat selection (Pugesek *et al.* 2003).

The emergence of multi-modal nesting patterns among smaller waterbird species further illustrates the complexity of breeding strategies in variable environments. Bimodal nesting behavior may represent a bet-hedging strategy that allows individuals to distribute reproductive

effort across multiple temporal windows, thereby reducing the risk of complete reproductive failure in unpredictable climatic conditions (Lack, 1954; Newton, 1998). At Kokkare-Bellur, the increasing occurrence of bimodal nesting over successive seasons likely reflects adaptive responses to fluctuating rainfall patterns, shifting prey availability, and changing competitive pressures within the colony (Both *et al.* 2006; Durant *et al.* 2007). Temporal partitioning of breeding effort may also reduce intra- and inter-specific competition, particularly when resource availability varies markedly within a season (Krebs, 2002).

The ecological patterns observed at Kokkare-Bellur are closely linked to the broader landscape context in which the colony is embedded. The absence of a large permanent wetland at the heronry suggests that breeding success depends on access to a dispersed network of rivers, irrigation tanks, seasonal wetlands, and agricultural fields. Such wetland networks allow waterbirds to track spatial and temporal variation in food resources and buffer against local resource depletion or hydrological instability (Harrison *et al.* 2010). Movement among interconnected wetlands may therefore play a crucial role in supporting extended breeding seasons and repeated nesting attempts. Maintaining connectivity among these habitats is essential for facilitating dispersal, enhancing gene flow, and increasing population resilience in the face of environmental change (Bélisle, 2005; Lindenmayer and Fischer, 2006).

The reliance on a network of wetlands also underscores the vulnerability of the system to habitat loss, hydrological alteration, and land-use change. Disruption of connectivity or degradation of key foraging habitats may amplify the effects of rainfall variability and density dependence, potentially leading to reduced reproductive success and long-term population declines (Dunn *et al.* 2006). In this context, the persistence of the Kokkare-Bellur heronry within a human-dominated landscape highlights the importance of culturally mediated protection and community tolerance in sustaining long-term breeding colonies (Subramanya, 1996; Urfi, 2011; Tryjanowski *et al.* 2013).

Long-term monitoring is essential for understanding and conserving such dynamic socio-ecological systems. Multi-year datasets allow researchers to distinguish between short-term fluctuations and long-term trends in breeding phenology, population size, and reproductive success, particularly in environments characterized by high climatic variability (Nichols and Williams, 2006). The patterns documented in this study could not have been reliably detected through short-term observations alone. Continued monitoring will be critical for assessing the impacts of increasing rainfall variability associated with climate change and for informing adaptive management strategies aimed at sustaining colonial waterbird populations (Runge *et al.* 2017).

3.5 Conclusion

This study provides a detailed evaluation of the role of rainfall in shaping nesting chronology and reproductive dynamics of colonial waterbirds in a human-modified landscape of southern India. Over five breeding seasons, clear links were established between monsoonal rainfall variability and species-specific nesting responses, reinforcing the role of precipitation as a dominant driver of breeding phenology in tropical wetland systems. The observed behavioral plasticity in nesting initiation and duration highlights the adaptive capacity of waterbirds to respond to fluctuating environmental conditions, while differences between larger and smaller species underscore the influence of life-history traits on breeding strategies.

The identification of density-dependent effects and multi-modal nesting patterns reveals how competition, resource limitation, and temporal variability interact to structure reproductive outcomes within mixed-species colonies. The dependence of breeding waterbirds on a dispersed network of wetlands further emphasizes the importance of landscape-scale processes and habitat connectivity in sustaining reproductive success, particularly in regions lacking large permanent wetlands.

Collectively, these findings highlight the complex interplay between climate variability, population dynamics, and landscape structure in determining the reproductive ecology of colonial waterbirds. In the context of increasing climatic uncertainty and ongoing habitat modification, conservation strategies must prioritize the protection of wetland networks, maintain hydrological integrity, and support long-term monitoring programs. Such integrated approaches will be essential for ensuring the persistence of ecologically and culturally significant heronries such as Kokkare-Bellur and for safeguarding waterbird populations under future environmental change.

Chapter – 4

Exploring nesting niche partitioning and sharing in colonial waterbirds

4.1 Introduction

Colonial waterbirds are a diverse and ecologically significant group of avian species characterized by their gregarious nesting behavior. These birds aggregate in dense colonies, often comprising thousands of individuals from multiple species, to breed and raise their young (Burger, 1981). Such communal nesting offers numerous advantages, including enhanced protection against predators through predator swamping and increased vigilance, as well as improved foraging efficiency through information sharing about food sources (Brown and Brown, 2001; Danchin and Wagner, 1997). However, these benefits come with ecological trade-offs. High-density breeding aggregations frequently lead to intense intra- and interspecific competition for essential resources, particularly suitable nesting sites and materials (Burger, 1979; Gopi and Pandav, 2011). The selection of appropriate nesting trees, therefore, becomes a crucial determinant of reproductive success and colony stability. Understanding the specific characteristics of trees chosen for nesting provides critical insights into the ecological drivers shaping the breeding distribution, habitat preferences, and interspecific interactions among colonial waterbirds (Urfi, 2011; Roshnath and Sinu, 2017; Frank *et al.* 2021).

In such crowded breeding, direct competition for shared nesting resources is minimized (Burger, 1979). Niche partitioning allows species to exploit different dimensions of their habitat, such as tree species, height, canopy density, or microhabitat features, thereby reducing resource-use overlap (Gond *et al.* 2013; Scherer *et al.* 2014). This ecological strategy becomes particularly important when closely related or ecologically similar species breed in proximity, as even subtle differences in nesting preferences can alleviate competitive pressures. For

colonial waterbirds, such differentiation often manifests through nest-site segregation or vertical stratification within nesting trees. The “nesting height–bird size hypothesis” further supports this idea, suggesting a positive relationship between a species’ body size and its nesting height, reflecting adaptive partitioning along the vertical axis of the nesting habitat (Burger and Gochfeld, 1990).

Evidence from recent studies further illustrates how colonial waterbirds across Asia employ such strategies to coexist within shared habitats. Ye *et al.* (2021), for example, documented spatial, temporal, and trophic segregation between two sympatric ardeids- Little Egret (*Egretta garzetta*) and Cattle Egret (*Bubulcus ibis*) in central China, and reported that Cattle Egret nested higher, bred later, and foraged in distinct habitats. Similar ecological dynamics have been observed in India. Abbasi and Khan (2023) examined four egret species: Great, Intermediate, Little, and Cattle Egrets, in a tropical wetland of northern India, and demonstrated that fine-scale differences in microhabitat use, foraging schedules, and dietary preferences facilitated their coexistence. These findings underscore that even morphologically similar species can minimize direct competition through partitioning along spatial and temporal axes. Similarly, Frank *et al.* (2021) studied mixed-species heronries in southern India and highlighted how nesting-tree characteristics, particularly height, canopy cover, and proximity to water, governed the vertical and spatial segregation of nests, emphasizing the role of habitat structure in maintaining colony diversity and stability.

While these studies primarily emphasize the ecological and structural aspects of coexistence, other research has focused on the socio-ecological settings that also shape colonial breeding systems. Kannan (2023), examined waterbird colonies embedded within human settlements in southern India, documenting how species such as Spot-billed Pelican (*Pelecanus philippensis*), Painted Stork (*Mycteria leucocephala*), and Black-crowned Night Heron (*Nycticorax nycticorax*) successfully breed in close proximity to people across sites such as Nelapattu,

Telineelapuram, Koonthankulam, and Kokkare-Bellur. Notably, surveys of heronries across India (Subramanya, 1996; 2001; 2005) revealed that over half of the country's known colonies occur within or near villages, demonstrating a long-standing tradition of human tolerance and community protection, although many of these sites have declined due to changing socio-cultural values (Manakadan and Kannan, 2003). However, such human-associated heronries stand in contrast to natural or protected-area colonies that occupy expansive wetland or forest habitats. Within village landscapes, nesting trees are often limited in number, spatially scattered, and subject to anthropogenic influences, conditions that could intensify competition for nesting space and alter traditional patterns of niche differentiation. This raises a compelling ecological question: in a spatially confined, human-modified environment such as Kokkare-Bellur, how do colonial waterbirds utilize and partition nesting resources to sustain coexistence?

This study focuses on the colonial waterbird population at the Kokkare-Bellur Community Reserve, a unique site where nesting trees are integrated within a small village landscape. This context presents a fascinating case study for examining how these species adapt their nesting preferences within a human-modified environment. The presence of nesting trees in discrete patches within the village highlights the importance of localized habitat features in supporting these large breeding aggregations. The long-term observation period, pooling nest data over five years (2018-2023) for five species, Spot-billed Pelican, Painted Stork, Black-crowned Night Heron, Little Egret, and Little Cormorant *Microcarbo niger*, provides a robust dataset for analyzing consistent patterns in nesting site selection.

Research Objectives and Hypotheses

Research Objective:

The primary objective of this study is to examine nesting niche partitioning and resource sharing among colonial waterbird species within a mixed-species breeding colony at Kokkare-Bellur, Southern India, with a focus on spatial organization, nesting density, vertical stratification, and tree species use.

- a) Are there discernible patterns of spatial segregation among colonial waterbird species during nesting within the colony?
- b) How do colonial waterbird species partition nesting niches while breeding within the same habitat?
- c) Do nesting species exhibit preference or avoidance trends for specific nesting tree species within the colony?

To address these questions, the study evaluates differences in nearest-neighbour distances within and between species, species-specific nesting densities, patterns of vertical stratification in nest placement relative to body size, and the distribution of nests across available tree species.

Hypothesis:

Colonial waterbird species exhibit clear nesting niche partitioning within mixed-species colonies to minimize interspecific competition and facilitate coexistence. It is hypothesized that species will differ significantly in spatial arrangement, with greater interspecific nearest-neighbour distances compared to intraspecific distances, reflecting varying levels of tolerance and competition. Nesting densities are expected to vary among species according to body size and space requirements, while vertical stratification within trees is anticipated to correspond with species' body size and ecological adaptations. Additionally, species are expected to show

non-random patterns of tree use, indicating preferences or avoidance linked to tree structure, stability, and proximity to water. Understanding these patterns will provide insight into mechanisms of coexistence in colonial waterbirds and inform habitat management and conservation strategies in human-dominated landscapes.

4.2 Methods

The Kokkare-Bellur Community Reserve is a unique and significant site for colonial waterbirds, and is located within a small village environment. This reserve is renowned for its long-standing tradition of co-existence between the local human population and nesting waterbirds, primarily the Spot-billed Pelican and Painted Stork, as well as other species. The nesting trees are not confined to a protected forest area but are rather scattered in patches within and around the village, making it an exemplary site for studying human–wildlife interactions and habitat use in an anthropogenic landscape. The villager’s commitment to protecting these birds, often viewing them as indicators of prosperity, has fostered a stable nesting environment. We collected detailed data on both nesting and non-nesting trees within the Kokkare-Bellur Community Reserve to identify the ecological and structural factors influencing tree selection for nesting.

Our dataset comprised 399 individual trees, representing all trees surveyed within the main nesting patches in the village landscape. The term *main nesting patch* refers to clusters of trees within the village limits whose canopies interconnect, forming a continuous patch used collectively by colonial waterbirds for nesting. The inclusion of both nesting and non-nesting trees allowed us to distinguish characteristics that define suitable nesting habitats from those that are not. For each tree, we recorded its spatial coordinates via a handheld GPS (Garmin 72, accuracy ± 3 m). We also noted tree species identity, girth at breast height (GBH), tree height (measured using a 20m marked pole), and canopy spread (estimated as the mean of two

perpendicular canopy diameters). For all nesting trees, we identified each nest to species level and recorded the number of nests per species. The pooled nest counts across the five breeding seasons (2018–2023) provided a cumulative measure of nesting activity for each tree, allowing us to capture consistent nesting preferences over time rather than year-specific fluctuations. Over this five-year period, a total of 6,786 nests were recorded across the five focal species, comprising 942 nests of Spot-billed Pelican, 4,096 nests of Painted Stork, 1,258 nests of Black-crowned Night Heron, 207 nests of Little Egret, and 283 nests of Little Cormorant. We created a binary response variable (“nest_flag”) to indicate the presence (1) or absence (0) of active nests on each tree. To examine the potential influence of anthropogenic proximity, we also measured the distance from each tree to the nearest road and to the nearest built-up area via satellite imagery in Google Earth Pro and QGIS 3.22. These landscape-level variables provide a measure of human disturbance and accessibility.

All the analyses were carried out in R version 4.5.1 (R Core Team 2024). To explore whether nests of different species were spatially aggregated and whether particular tree patches were preferred, we first performed unsupervised clustering of the nesting-tree coordinates via the K-means algorithm. We determined the optimal number of spatial clusters (k) via the elbow method (Kassambara, 2017). For each cluster, we calculated the relative abundance and species composition to identify any patterns of spatial segregation among the dominant nesting species. We further visualized the nesting space by generating Kernel Density Estimation (KDE) heatmaps for each species (Spurr, 2003). These maps illustrated areas of high nest density, allowing us to qualitatively assess spatial overlap and segregation in nest distribution within the village landscape.

To investigate how tree structural and environmental characteristics influence nesting, we used Non-metric Multidimensional Scaling (NMDS) on scaled tree-level variables (tree height, GBH, canopy spread, distance to roads, and distance to built-up areas). NMDS is a non-

parametric ordination method suitable for non-normal ecological data (Minchin, 1987). We fitted environmental vectors to the ordination via the `envfit` function to identify which variables most strongly correlated with the nesting patterns of the species. To statistically evaluate whether the dominant nesting species differed in their use of tree characteristics, we conducted PERMANOVA (`adonis2`) analysis on the tree attribute matrix. This approach allowed us to test for significant multivariate differences in nesting-tree structure among species. We modeled the probability of a tree being used for nesting via a generalized linear model (GLM) with a binomial error structure. Because some tree species were either exclusively used or entirely avoided by particular bird species, the data exhibited quasi-complete separation. To address this, we applied Firth's penalized logistic regression (Heinze and Schemper, 2002) via the *logistf* package in R. The predictors included tree structural variables (height, GBH, canopy spread), landscape variables (distance to road, distance to built-up area), and tree species identity. We exponentiated the model coefficients to obtain odds ratios (Ors), which indicate the strength and direction of the associations between the predictors and the nesting probability. OR values greater than 1 denote a positive association with likelihood of nesting, whereas values less than 1 indicate avoidance. Statistical significance was determined via penalized likelihood ratio tests.

To assess potential interspecific differences in nearest neighbor distance (NND), nest density, and nest height, we first tested for normality via the Shapiro–Wilk test and for homogeneity of variances via Levene's test. Because the data violated both assumptions, we used the Kruskal–Wallis rank-sum test to compare medians among species, followed by Dunn's post-hoc test with Holm-adjusted p -values for pairwise comparisons (Dunn, 1964; Holm, 1979). We defined nest density as the total number of nests per tree for each species. For vertical nest stratification analysis, we compared nest heights among species via the same non-parametric framework. We further examined the relationship between average body size (as an indicator of

morphological scaling) and mean nest height across species via Pearson's correlation, testing the "nesting height–body size" hypothesis.

4.3 Results

K-means clustering analysis revealed four distinct spatial clusters ($k=4$) of nesting trees, indicating prominent spatial groupings within the study site (Fig. 4.1). While each cluster contained nests from multiple species, suggesting broad-scale cohabitation, a closer look revealed subtle spatial partitioning. For example, Clusters 2 and 3 were strongly dominated by Painted Storks and Black-crowned Night Herons, respectively. The Spot-billed Pelican appeared more aggregated in the north-eastern clusters, possibly due to the selection of less disturbed patches. In contrast, the Little Cormorants and Little Egrets were more scattered. This finding demonstrates that, although the species are not segregated into single-species colonies, they do show preferences for specific spatial patches, indicating that habitat patch use reduces interspecific competition.

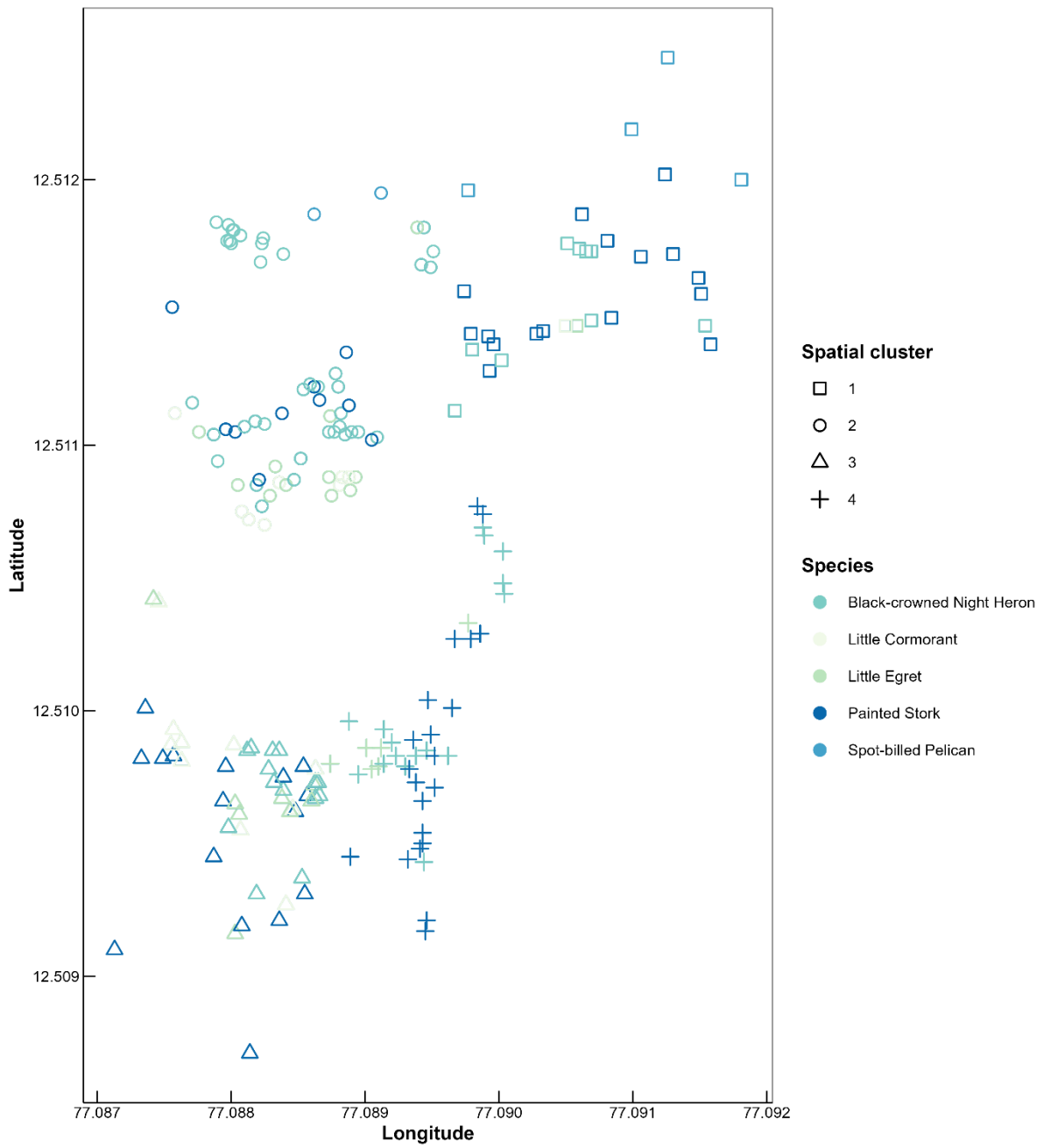


Figure 4.1 Clustering of nesting trees based on spatial coordinates using k-means. Each color represents a distinct species and distinct shape represent spatial cluster.

The kernel density heatmaps provided a fine-scale view of spatial preferences and overlap (Fig. 4.2). They revealed a high degree of spatial overlap, particularly between Cormorant and Egret, whose heatmaps were nearly identical, showing dense nesting concentrations in the same two primary locations. A similar high overlap was observed between Painted Storks and Night Herons. Conversely, Pelican formed a distinct cluster in the northern and eastern portions of the site, with only sparse overlap with other species. This suggests that, while overall coexistence is the norm, species often maintain core, high-density nesting zones that are spatially distinct, reflecting niche partitioning at the microhabitat scale.

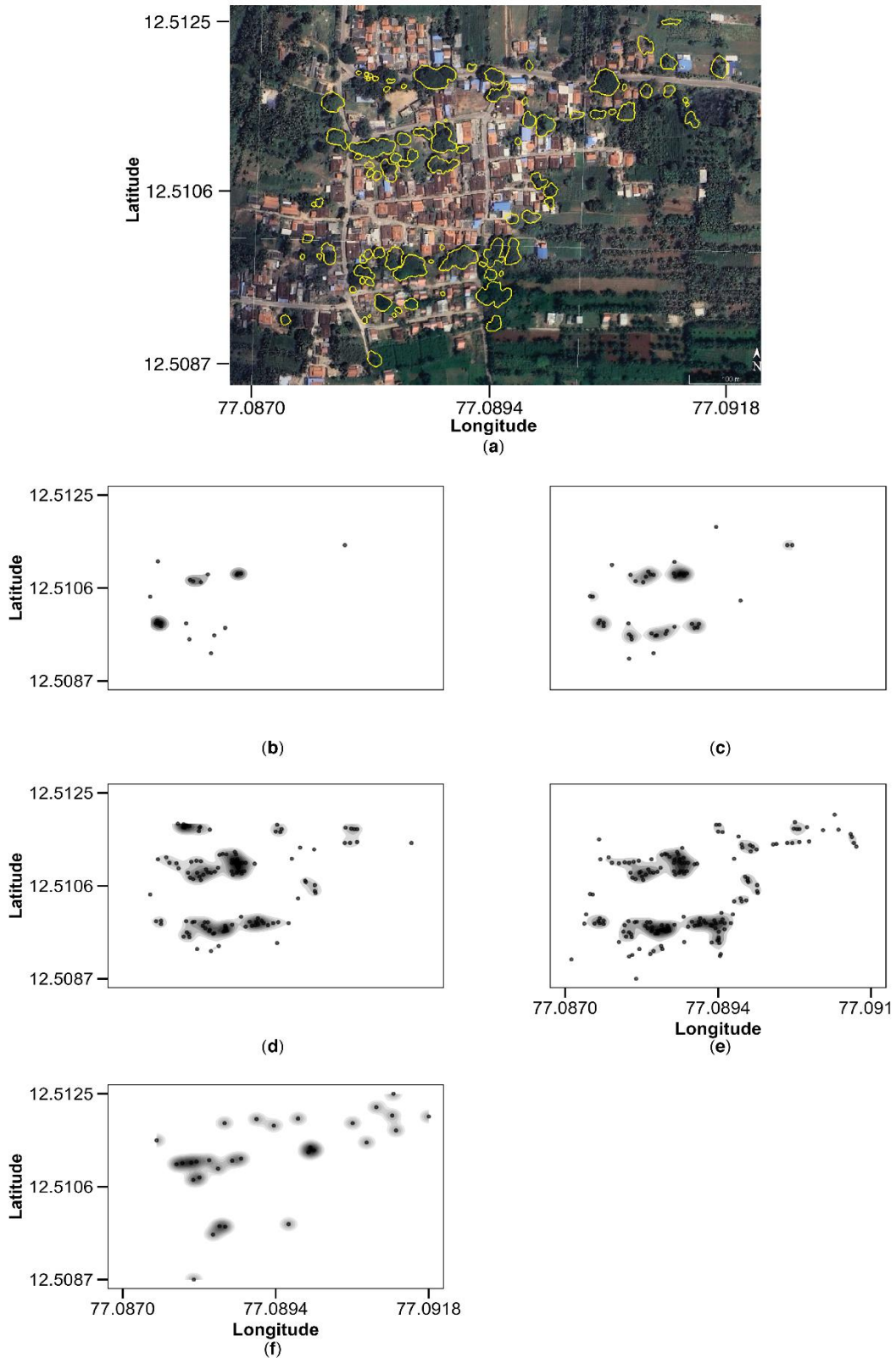


Figure 4.2 Spatial context and species-specific nesting space use of colonial waterbirds in Kokkare-Bellur village. (a) Google Earth image of Kokkare-Bellur village, providing spatial context for the nesting tree patches. Panels (b–f) show kernel density estimation

(KDE) heatmaps representing species-specific nesting space use within the village, where darker shading indicates higher nest density. Species shown are: (b) Little Cormorant, (c) Little Egret, (d) Black-crowned Night Heron, (e) Painted Stork, and (f) Spot-billed Pelican.

The nesting preferences revealed that waterbirds do not randomly select nesting sites. A small number of tree species, particularly *Thespesia populnea* and *Tamarindus indica*, account for the vast majority of nesting activity. Conversely, 12 species, including *Eucalyptus* and *Tectona grandis*, were completely avoided (Table 4.1). A Non-Metric Multidimensional Scaling (NMDS) ordination was performed on the scaled tree habitat variables. The 2-dimensional NMDS solution had a stress value of 0.182, indicating observed dissimilarities in reduced dimensional space. An environmental fitting (envfit) procedure identified five environmental variables with the strongest and most significant correlations: tree height ($r^2= 0.69$), GBH ($r^2= 0.67$), canopy spread ($r^2= 0.63$), canopy cover ($r^2= 0.57$), and nearest distance to built-up area ($r^2= 0.43$). Species such as the Spot-billed Pelican and the Painted Stork were more strongly associated with sites of taller trees, greater GBH, and broader canopy spread. In contrast, Cormorants were more aligned with areas closer to built-up infrastructure. Egrets and Night Herons presented broader ecological tolerances across these gradients (Fig. 4.3). PERMANOVA (adonis2) analysis further confirmed these findings. The model indicated that the dominant species variable explained 8.76% of the variation in nesting tree characteristics ($r^2=0.08$). The F-statistic ($F=4.486$) and a highly significant p-value ($p=0.001$) revealed that the differences in the multivariate centroid locations of the species were not due to chance, confirming that tree structural characteristics vary significantly among the dominant nesting species.

Table 4.1. Species-wise distribution of trees recorded at Kokkare-Bellur village, categorized by presence and absence of colonial waterbird nesting activity, indicating relative nesting preference across tree species.

Tree species	Trees without nest (n)	Trees with nest (n)	Total Trees (n)
<i>Thespesia populnea</i>	30	89	119
<i>Delonix elata</i>	34	32	66
<i>Tamarindus indica</i>	3	25	28
<i>Ficus benghalensis</i>	1	12	13
<i>Ficus religiosa</i>	11	8	19
<i>Samanea saman</i>	13	5	18
<i>Cassia fistula</i>	0	5	5
<i>Holoptelea integrifolia</i>	9	3	12
<i>Grevillea robusta</i>	1	2	3
<i>Ficus mysorensis</i>	0	2	2
<i>Acacia nilotica</i>	1	2	3
<i>Commiphora caudata</i>	24	1	25
<i>Pongamia pinnata</i>	7	1	8
<i>Azadirachta indica</i>	11	1	12
<i>Artocarpus integrifolia</i>	3	1	4
<i>Albizia amara</i>	0	1	1
<i>Albizia lebbek</i>	0	1	1
<i>Areca catechu</i>	0	1	1

Tree species	Trees without nest (n)	Trees with nest (n)	Total Trees (n)
<i>Eucalyptus sp., Tectona grandis, Saraca asoca, Melia dubia, Cocos nucifera, Muntingia calabura, Delonix regia, Wrightia tinctoria, Caica papaya, Mangifera indica, Moringa oleifera, Syzygium cumini</i>	59	0	59

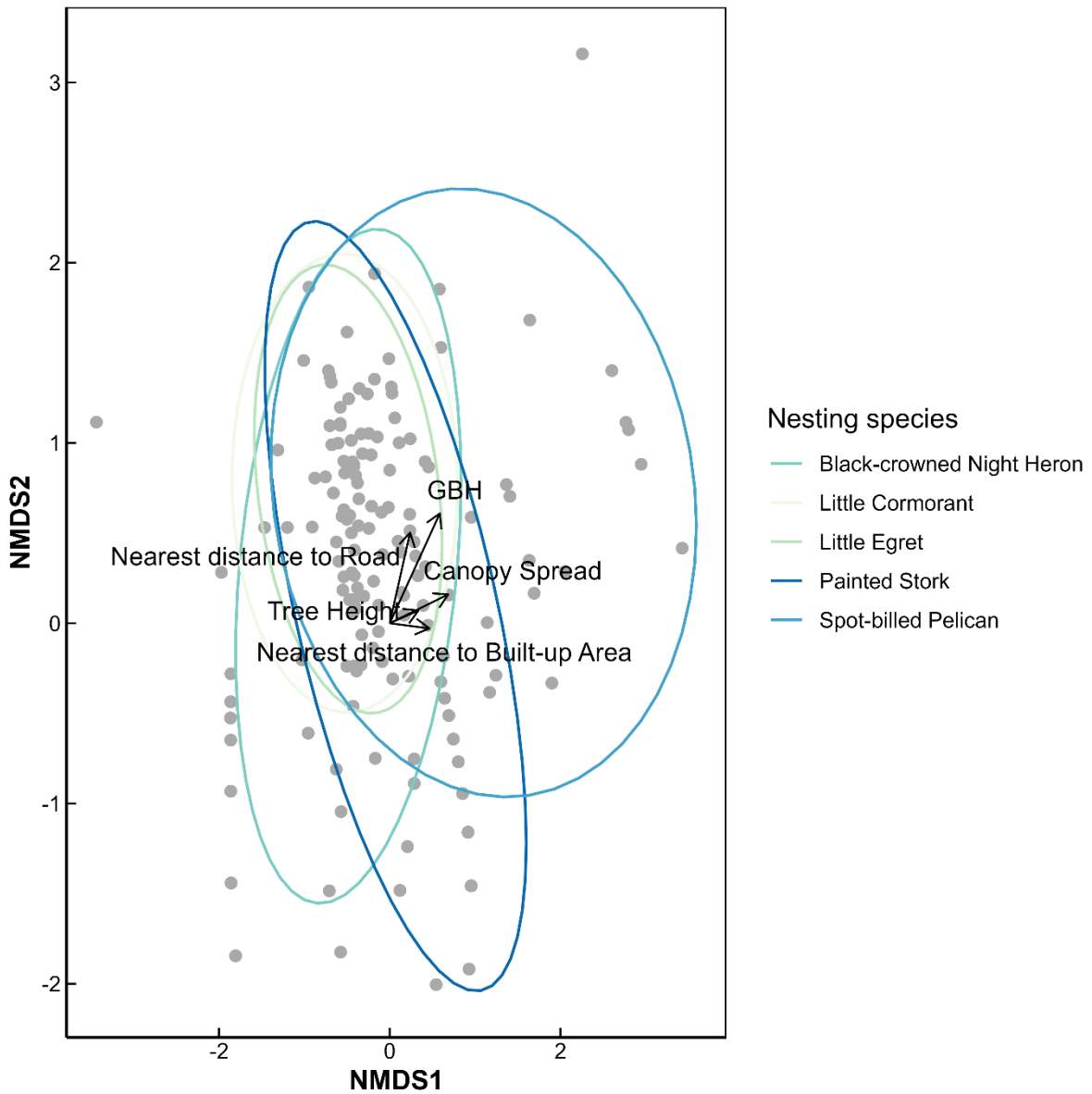


Figure 4.3 NMDS ordination of nesting tree sites based on the presence of five colonial waterbird species- Little Cormorant, Little Egret, Black-crowned Night Heron, Painted Stork, and Spot-billed Pelican, via Jaccard dissimilarity. Points represent individual nesting trees, while colored ellipses (95% confidence intervals) indicate species-specific clustering and overlap in nesting habitat use. Arrows denote the five most influential environmental variables fitted using envfit, with arrow length proportional to the strength of correlation with the ordination axes. The ordination is displayed in

two dimensions ($k = 2$); stress value indicates the goodness-of-fit of the NMDS solution.

The penalized logistic regression model identified several key predictors of nesting probability and showed a significant improvement over the null model (likelihood ratio test = 221.28, $df = 35$, $p = 0$), indicating that the combination of tree morphology and landscape context drives nesting site selection. GBH emerged as a strong positive predictor of nesting probability (odds ratio = 1.01, $p < 0.05$), reflecting a clear preference for larger and structurally more stable trees. Canopy cover also showed a significant positive association with the likelihood of nesting (odds ratio = 1.02, $p < 0.05$), suggesting that trees with denser foliage are favored as nesting substrates. In contrast, canopy spread was a significant negative predictor (odds ratio = 0.98, $p < 0.05$), indicating selection for trees with compact, densely branched canopies rather than those with broad horizontal spread. Distance to built-up areas was likewise negatively associated with probability of nesting (odds ratio = 0.97, $p < 0.05$), demonstrating that trees located closer to human habitation were more likely to be used for nesting. In addition to these structural and landscape effects, the model provided strong evidence for species-level avoidance, with certain tree species, notably *Tectona grandis* (odds ratio = 0.005) and *Saraca asoca* (odds ratio = 0.006), being actively avoided as nesting sites.

Nesting tree preferences for the five focal species were analyzed via forest plots (Fig. 4.4), which depict the selection of nesting sites relative to tree availability in the village landscape. The analysis revealed that particular tree species, although rare in the area, with only a single individual present, were disproportionately used for nesting, indicating strong species-specific preferences. Spot-billed Pelicans exhibited a marked affinity for *Ficus benghalensis* and *Tamarindus indicus*, suggesting a reliance on large trees for colony establishment. Storks, while generally more flexible in their nesting choices, showed a notable preference for *Albizia*

amara. Both Egrets and Cormorants appeared to be generalist nesters, utilizing a wide range of tree species; however, both groups tended to select *Albizia* spp. and *Areca catechu* as preferred nesting substrates. In contrast, Night Herons displayed distinct selectivity, predominantly nesting in *Cassia fistula* and *Ficus mysorensis*, indicating specific structural or microhabitat requirements associated with these species.

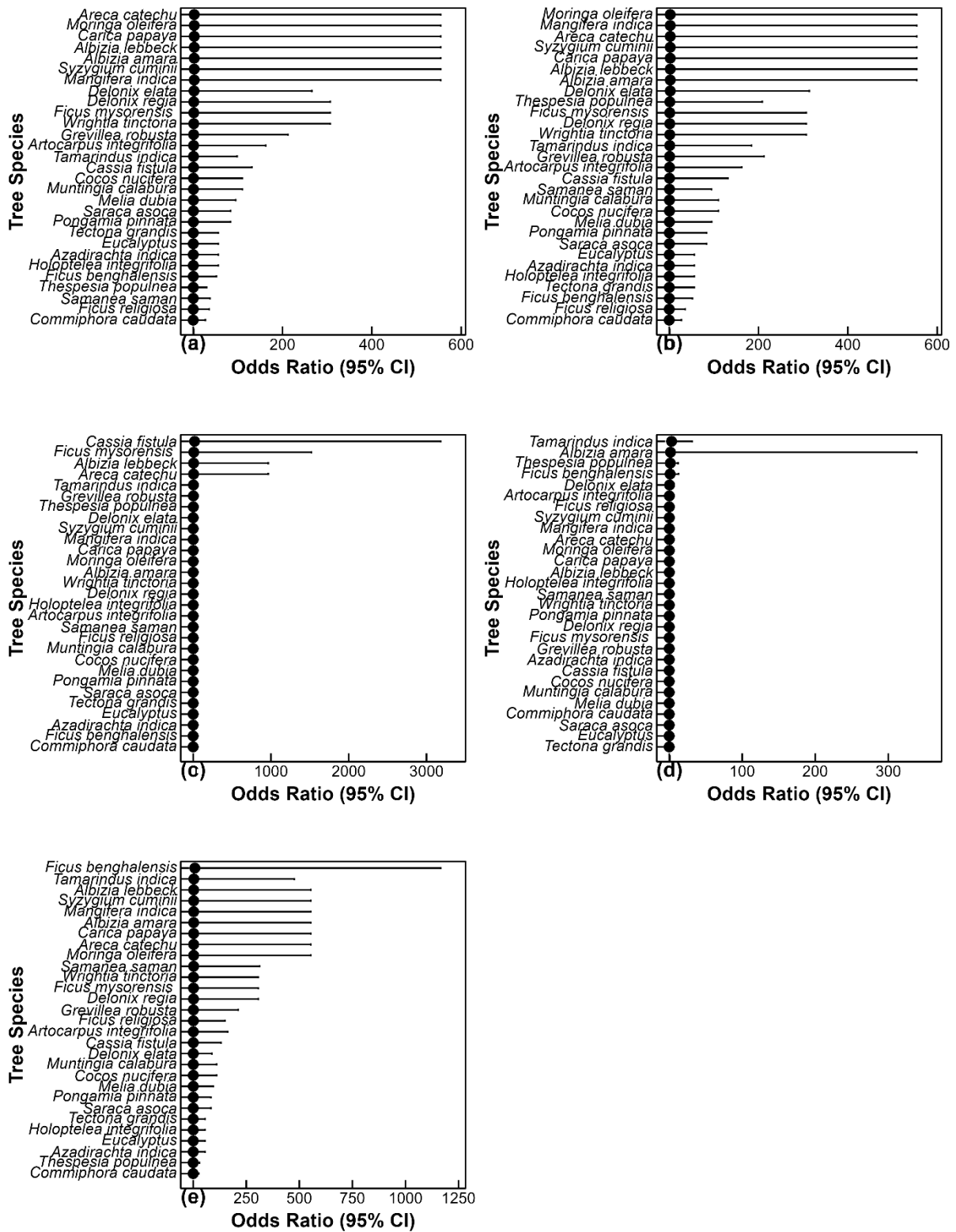


Figure 4.4 Species-specific forest plots showing nesting tree preferences of five colonial waterbird species. Odds ratios (with 95% confidence intervals) from Firth's logistic regression indicate the relative likelihood of nest occurrence on different tree species

for (a) Little Cormorant, (b) Little Egret, (c) Black-crowned Night Heron, (d) Painted Stork, and (e) Spot-billed Pelican. The vertical dashed line denotes an odds ratio of 1 (no effect).

The Kruskal-Wallis test revealed a highly significant difference in nearest neighbor distance (NND) between species ($\chi^2=724.43$, $df=4$, $p<0.05$). Post-hoc Dunn's tests revealed that nearly all the species pairs differed significantly. Spot-billed Pelicans presented the smallest median NND (~0.3 m), indicating highly clustered nest placement. In contrast, Little Egrets had the largest median NND (~2.0 m), followed by Black-crowned Night Herons (~1.4 m) (Fig. 4.5). These findings suggest that species-specific behaviors and body sizes play crucial roles in horizontal spatial partitioning. The Kruskal-Wallis test also revealed a significant difference in nest density among species ($\chi^2=18.647$, $df=4$, $p=0.0009$). Dunn's post-hoc tests indicated that Little Egrets presented significantly lower mean nest densities than other species did. No significant differences were found between Cormorant, Night Heron, Pelican, and Stork after p-value adjustment. Pelican shows the highest variability in density, with some extreme outliers reaching nearly 90 nests per tree. The median density for pelicans is relatively high compared with that of other species, indicating that pelicans often nest in large colonies. Cormorant also has a relatively high median density (approximately 8–10 nests per tree) with a few trees containing over 40 nests, suggesting moderately large group nesting. Storks have a moderate median density but widespread, including some trees with 40–50 nests, indicating that storks sometimes nest in large aggregations. Night Heron had a moderate median density (similar to stork) but a slightly lower spread, with fewer extremely high-density cases. On the other hand, Little Egret had the lowest median density (approximately 2–3 nests per tree) and the smallest spread, indicating that it generally nests more sparsely than other species do (Fig. 4.6). Analysis of nest height revealed a clear pattern of vertical stratification within the colony, with species

nesting at different heights on the basis of their body size. The five study species varied significantly in body length: pelican (152 cm), stork (102 cm), night heron (66 cm), egret (65 cm), and cormorant (55 cm). The Kruskal-Wallis rank-sum test revealed a highly significant difference in nest height among the five species ($\chi^2=673.26$, $df=4$, $p<0.05$). Post-hoc Dunn's tests further confirmed that almost all the species nested at significantly different mean heights from one another. Spot-billed Pelicans nested at the greatest heights, significantly greater than that of all the other species. The Painted Storks, which are large-bodied birds, nested in upper strata, are similar to Pelicans. Little Cormorants occupied the lowest mean nesting heights, which were significantly lower than those of all the other species. Little Egrets and Black-crowned Night Herons nested at intermediate heights, and their nest heights differed significantly from each other, with Night Herons nesting slightly higher on average (Fig. 4.7). A strong and positive Spearman's rank correlation was found between the mean adult body length of the species and their mean nest height ($\rho = 1$, $p<0.05$). This indicates a perfect monotonic relationship: as a species' body size increases, its average nesting height also increases.

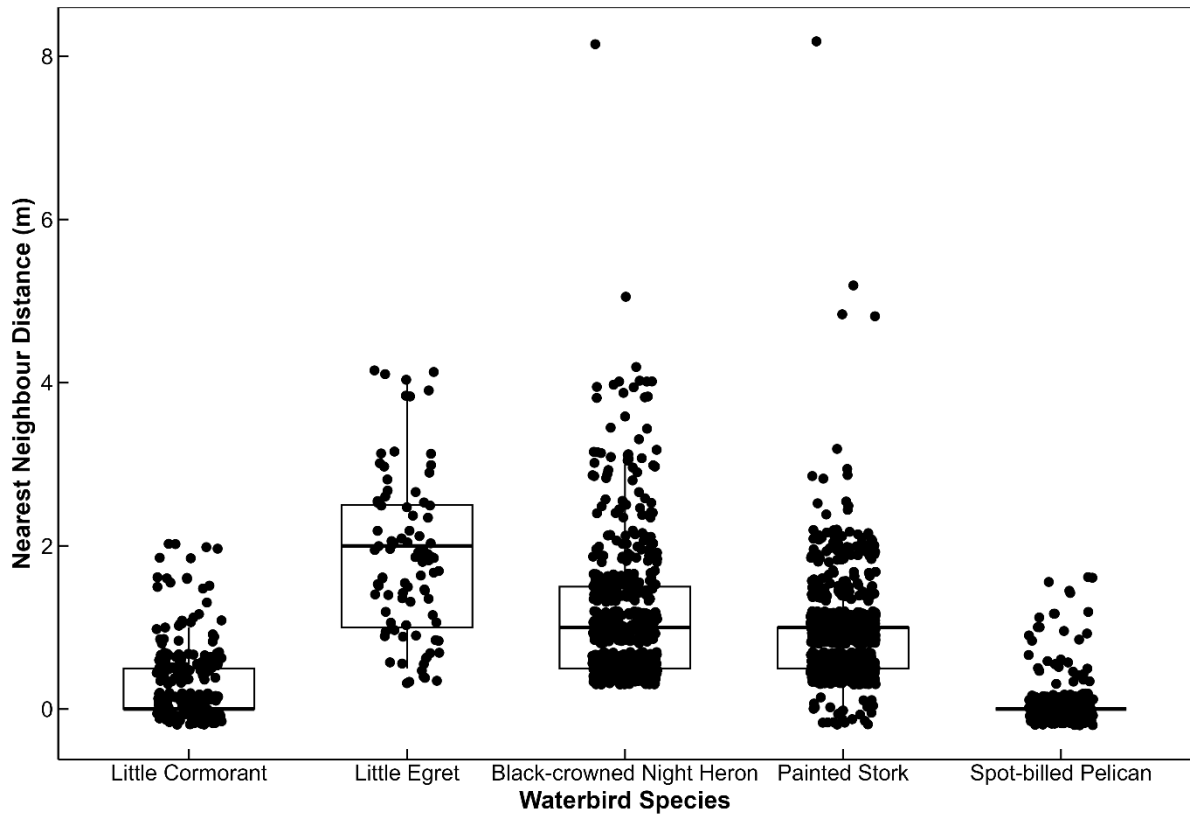


Figure 4.5 Variation in nearest neighbor distance (NND, m) among five waterbird species.

Boxplots indicate the median and interquartile range, with points representing individual nest-level observations.

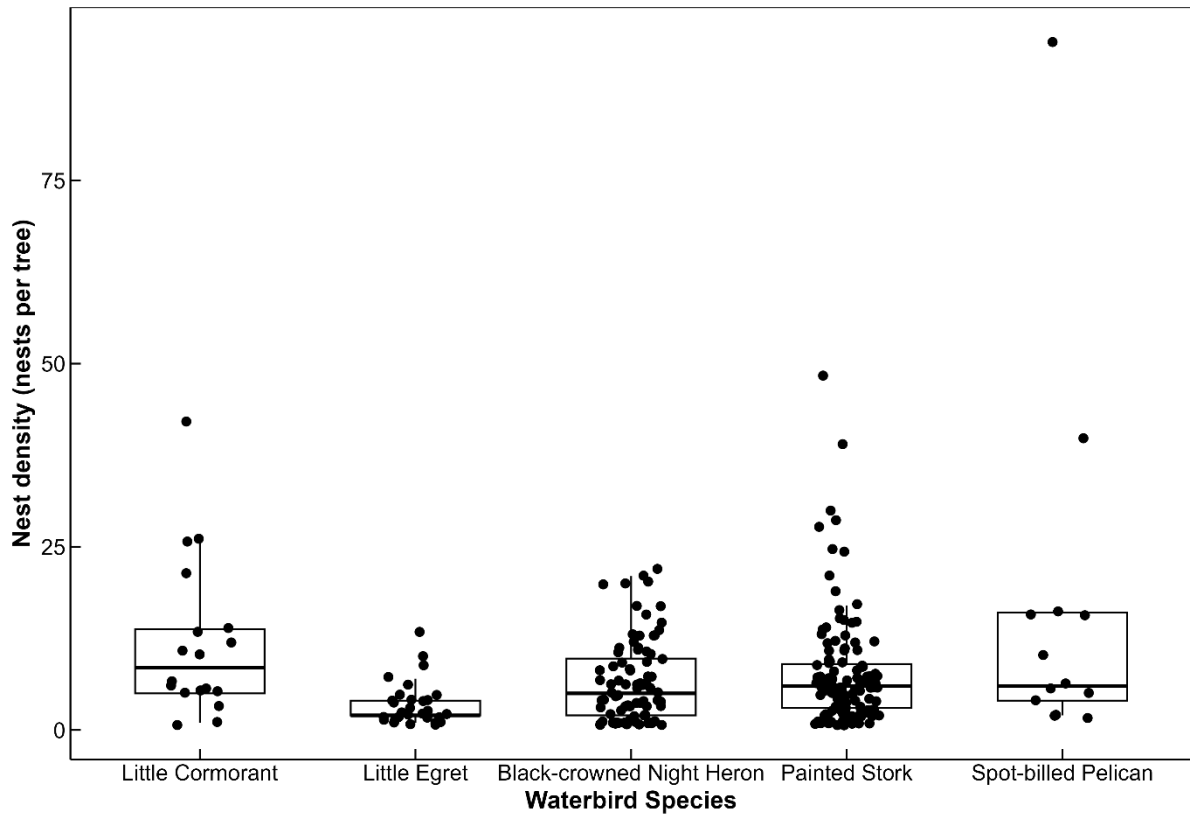


Figure 4.6 Differences in nest density (number of nests per tree) among five waterbird species.

Boxplots indicate the median and interquartile range, and points show tree-level observations.

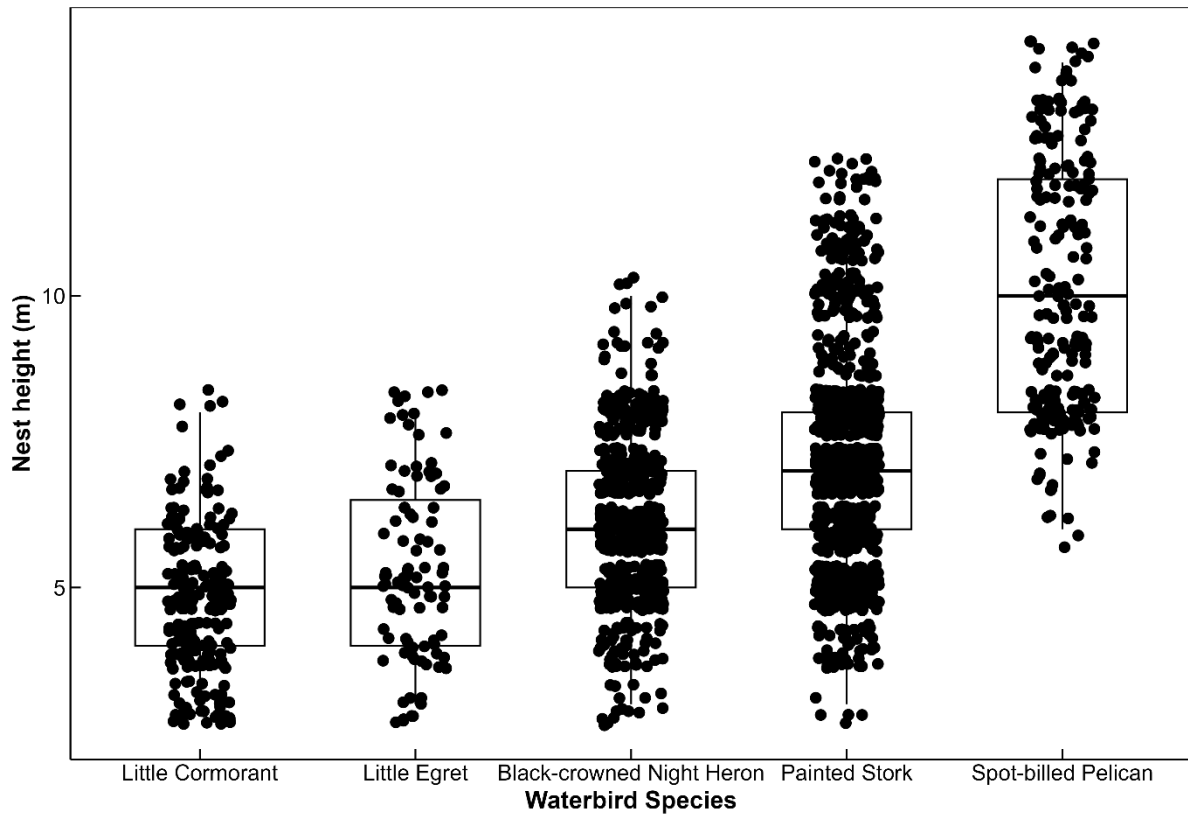


Figure 4.7 Vertical stratification of nesting, expressed as nest height (m), among five waterbird species. Boxplots represent the median and interquartile range, with points indicating individual nest observations.

4.4 Discussion

This study provides a comprehensive analysis of nesting niche partitioning and sharing among five colonial waterbird species in the unique, human-modified landscape of the Kokkare-Bellur Community Reserve. These findings demonstrate that, while these species coexist within a shared habitat, they employ distinct strategies to partition resources, primarily by selecting specific nesting sites on the basis of a combination of spatial, morphological, and structural characteristics. This differential resource selection is a principal factor that permits species to coexist in a shared environment (Schoner, 1974; Rosenzweig, 1981).

Our results confirm that nesting tree selection is non-random, with a clear preference for a few tree species, notably, *Thespesia populnea* and *Tamarindus indica*. This finding corroborates

the literature on colonial waterbirds, which often highlights the importance of specific tree species in supporting large breeding aggregations due to their structural suitability (Urfi, 2011; Gond *et al.* 2013). This preference for certain trees, such as *Tamarindus indica*, aligns with observations from other heronries in southern India where these trees, often located along roadsides or on temple premises, provide excellent nesting habitats for smaller species such as the Little Cormorant and Little Egret (Frank *et al.* 2021). The complete avoidance of 12 tree species, such as *Eucalyptus* and *Tectona grandis*, reflects their unsuitability, possibly due to poor canopy structure or low stability. The strong positive relationship with GBH suggests a fundamental requirement for structural stability. Larger, older trees with thicker trunks and branches likely provide a more robust platform to support the heavy, aggregated nests of a colonial breeding site (Gopi and Pandav, 2011; Urfi, 2011). The preference for dense canopies provides essential concealment from aerial predators and protection from direct solar radiation, contributing to a stable microclimate for nestlings. The simultaneous negative association with canopy spread is not a contradiction but rather a key insight into the specific tree architecture preferred by these birds. This finding suggests a selective preference for a compact, densely branched, and foliated canopy that offers a robust, focused support structure, as opposed to a simple, broad one that may lack the necessary interlocking branches. The Non-Metric Multidimensional Scaling and PERMANOVA revealed significant differences in the use of trees and landscape characteristics among the species. For example, the larger-bodied Pelican and Stork showed a strong preference for taller trees with greater GBHs, whereas the Cormorant were more closely associated with areas closer to human habitation. This suggests a form of spatial niche partitioning in which different species exploit distinct microhabitats within the broader reserve. The tendency of Pelicans to aggregate in north-eastern, presumably less-disturbed, patches support the idea of spatial segregation at the macro-scale, as observed

in other colonial species that form distinct sub-colonies to reduce intraspecific and interspecific competition (Burger, 1979).

One of the most compelling findings is the significant preference for nesting sites located closer to human settlements. While human presence often acts as a disturbance, the unique socio-ecological system at Kokkare-Bellur presents a different narrative. The proximity to human habitation likely creates a "human shield" effect, deterring ground predators such as dogs, and snakes and reducing human-induced threats. This highlights a rare example of a mutualistic relationship where the birds have adapted to select sites where they are implicitly under human protection, and the villagers, in turn, actively protect them (Subramanya, 1996).

The most compelling evidence for niche partitioning in this study comes from the clear pattern of vertical stratification of nests within the colony. The strong positive correlation between a species' body size and its mean nesting height is a classic example of resource partitioning, which is consistent with the "nesting height-bird size hypothesis" (Burger and Gochfeld, 1990). The observed pattern with Pelicans and Storks occupying the highest strata, followed by intermediate-sized Egrets and Night Herons, and finally the smaller Cormorant at the lowest heights, is corroborated by findings from other mixed heronries in southern India (Kumar *et al.* 2009). This phenomenon is an evolutionary adaptation that mitigates the harmful effects of interspecific competition (Naugle *et al.* 1996). This vertical arrangement has also been attributed to aggressive dominance by larger species and their earlier arrival times at nesting sites (Burger, 1979; 1981; McCrimmon, 1978). The varying nearest-neighbor distances also highlight species-specific nesting behaviors. The highly clustered nests of Pelicans and Cormorants indicate a preference for high-density group nesting, which can provide benefits such as predator swamping. In contrast, the more dispersed nesting of Egrets suggests a different social strategy. Despite the clear evidence of partitioning, the study also highlights significant niche sharing. The kernel density heatmaps revealed a high degree of spatial

overlap, particularly between Cormorants and Egrets, and between Storks and Night Herons. This suggests that while species may partition resources vertically or on the basis of tree morphology, they often share the same general patches of habitat. This finding is further supported by the statistical similarity in nest density among several species, indicating that many of them tolerate similar levels of conspecific and heterospecific nesting proximity within a tree. This coexistence is a key feature of mixed-species colonies and may be facilitated by the superabundance of suitable nesting sites, a feature observed in other heronries (Kumar *et al.* 2009; Gopi and Pandav, 2011; Gond *et al.* 2013). The ability of these species to coexist, despite their spatial and nesting preferences, suggests a dynamic balance between competition and resource availability. This is particularly relevant in a human-modified landscape such as Kokkare-Bellur, where resource availability may be less predictable.

4.5 Conclusion

This study demonstrated that colonial nesting waterbirds at Kokkare-Bellur employ a combination of niche partitioning and niche sharing to enable their coexistence within a shared habitat. Despite overlapping in space, these species effectively segregate resources through several mechanisms. First, they exhibit selective use of specific tree species and structural attributes, showing a strong preference for large, robust trees with dense canopies and high GBH, often located near built-up areas. Second, a distinct pattern of vertical stratification by body size was observed, with larger species nesting at greater heights, providing clear evidence of resource partitioning as a means of reducing interspecific competition for nesting sites. Finally, spatial patch preferences were apparent, as some species, notably the Spot-billed Pelican, tended to occupy distinct clusters within the nesting landscape, indicating a broader-scale partitioning of habitat space. Together, these strategies highlight the complex ecological interactions that facilitate the stable coexistence of multiple colonial waterbird species within a limited nesting environment.

This research contributes to the understanding of community ecology in fragmented, human-dominated landscapes. The long-term stability of the Kokkare-Bellur colony is likely a direct result of these evolved behavioral strategies, which allow multiple species to thrive in a limited habitat. These findings have direct implications for the long-term conservation of the Community Reserve. Conservation efforts should prioritize the protection of mature trees with the desired structural characteristics: high GBH and dense, compact canopies. The results also underscore the critical importance of the human dimension in conservation, emphasizing the need for continued engagement and education of the local community to maintain the protective environment that benefits birds. Future research should expand on these findings by conducting species-specific analyses of nesting preferences to uncover finer-scale differences. Investigating additional unmeasured variables, such as specific branch angles or leaf characteristics, could provide a more complete understanding of the architectural features that influence nesting decisions. A deeper exploration of the socio-ecological dynamics of the "human shield" effect through ethnographic studies would also be a valuable, offering a model for human-wildlife coexistence in other contexts.

Chapter – 5

INVESTIGATING THE ECOLOGICAL DYNAMICS INFLUENCING THE NEST SURVIVAL RATE IN COLONIAL WATERBIRD SPECIES NESTING AT KOKKARE-BELLUR

5.1 Introduction

Colonial breeding in waterbirds represents a fundamental ecological trade-off between the benefits of social aggregation, such as enhanced predator defense and foraging efficiency, and the costs of intensified competition and disease transmission (Wittenberger and Hunt, 1985; Brown and Brown, 2001). The resolution of this trade-off is ultimately reflected in nesting success, a key demographic parameter that integrates the complex effects of phenology, environmental conditions, and social dynamics. Understanding the determinants of nesting success is therefore crucial for modeling population viability and developing effective conservation strategies, particularly for species of conservation concern (Tiwary and Urfi, 2016). The reproductive outcome for a given nest is not determined by any single factor in isolation but rather by their complex interplay: the timing of breeding (phenology) must align with seasonal resource pulses, while the choice of nest site must balance the benefits of social aggregation against the risks of predation and competition (Burger, 1979; Frederick and Loftus, 1993).

The timing of nest initiation is often critical, as early nesters may gain access to superior resources and favorable conditions, although this pattern can vary among species (Tiwary and Urfi, 2016). Spatial factors, such as colony size and nest density, can influence success through the benefits of coloniality, while specific nest-site characteristics like height and concealment can mediate predation risk and exposure (Burger, 1979). Furthermore, environmental conditions play a paramount role. Inclement weather can lead to direct mortality of vulnerable

nestlings (Griebel *et al.* 2019), while climatic variables such as temperature and precipitation indirectly shape reproductive outcomes by regulating the availability and accessibility of aquatic prey (Kushlan, 1986; Frederick and Loftus, 1993). For piscivorous birds, annual and seasonal precipitation patterns are particularly influential, as they drive the productivity of wetland foraging habitats (Urfi, 2011; Tiwary and Urfi, 2016).

Globally, colonial waterbird populations face increasing threats from habitat loss, pollution, and human disturbance, making studies on their reproductive ecology essential for conservation. In India, the conservation landscape for these species is particularly complex. A significant proportion of the country's heronries are situated not in remote, protected wetlands, but within or adjacent to human-dominated landscapes such as villages and urban parks (Subramanya, 1996; Urfi, 2011). This close association presents a unique conservation paradigm. On one hand, these heronries face intensified threats from habitat degradation, direct disturbance, and the loss of nesting trees due to urbanization and changing land-use practices (Manakadan and Kannan, 2003; Sundar, 2004). On the other hand, the continuous human presence may offer an inadvertent shield from natural predators, a phenomenon that remains poorly quantified in these systems. This context creates a critical need to understand how diverse waterbird species successfully breed under such complex and often conflicting pressures.

While studies in India have begun to document these patterns, research has often focused on niche partitioning dynamics (Frank *et al.* 2022; Abbasi and Khan, 2023) or the reproductive success of single, focal species (e.g., Painted Stork *Mycteria leucocephala*; Tiwary and Urfi, 2016). Consequently, a synthetic understanding of how a diverse assemblage of sympatric species navigates these interacting pressures to achieve reproductive success remains a critical knowledge gap. Without a multi-species perspective, it is difficult to ascertain whether the factors driving success are universal, or if species-specific strategies allow for coexistence

through differential responses to environmental and social cues. Answering this question is paramount for the holistic conservation of entire heronry communities.

To address this gap, we investigated the factors governing nesting success in a multi-species waterbird assemblage at the Kokkare-Bellur Community Reserve in southern India. This site provides an exemplary natural laboratory for this inquiry, representing a centuries-old tradition where large breeding aggregations of five sympatric species, including the near-threatened Spot-billed Pelican *Pelecanus philippensis*, nest within the village matrix. This unique setting allows for a robust examination of how diverse species respond not only to the overarching influence of the South Asian monsoon and the intrinsic dynamics of coloniality but also to the subtle and direct pressures of a human-inhabited landscape.

Research Objectives and Hypotheses

Research Objective:

The primary objective of this study is to investigate the ecological and spatial factors influencing nest survival rates of colonial waterbird species breeding at Kokkare-Bellur, Southern India, with emphasis on temporal variation, colony size, breeding phenology, and nest placement characteristics.

- a) How does nest survival vary temporally within and between breeding seasons among colonial waterbird species at Kokkare-Bellur?
- b) Does tree patch size, as a proxy for colony size, influence nest survival rates of colonial waterbird species?
- c) How does the timing of arrival and nest initiation influence nest survival rates among breeding individuals?

d) How do nest placement characteristics, including nest height, nearest-neighbour distance, and nesting density, influence nest survival rates?

Hypothesis:

Nest survival rates of colonial waterbird species are shaped by a combination of temporal, spatial, and behavioral factors operating within breeding colonies. It is hypothesized that nest survival will vary significantly within and between breeding seasons, reflecting fluctuations in climatic conditions, predation pressure, and anthropogenic disturbance. Larger tree patches and colony sizes are expected to be associated with higher nest survival due to predator dilution effects, although increased competition and aggression may offset these benefits at higher densities. Early-arriving individuals are predicted to exhibit higher nest survival by securing higher-quality nesting sites, while nest placement characteristics such as greater nest height, optimal nearest-neighbor distances, and moderate nesting densities are expected to enhance survival by reducing predation risk and environmental exposure. Evaluating these relationships will improve understanding of the drivers of reproductive success in colonial waterbirds and support evidence-based conservation and habitat management strategies in human-dominated landscapes.

5. 2 Methods

We conducted our research from October 2018 to September 2023 at the Kokkare-Bellur Community Reserve, a significant mixed-species heronry in southern India. This site is particularly important for its large breeding populations of the globally near-threatened Spot-billed Pelican (*Pelecanus philippensis*) and Painted Stork (*Mycteria leucocephala*). The reserve offers a unique study system where nesting trees are not in a secluded protected area but are woven into the fabric of a human village, found in residential yards, on agricultural

lands, and around temple grounds. This long-standing tradition of coexistence between villagers and waterbirds provides an exceptional setting for investigating colonial waterbird ecology in an anthropogenic landscape. Our investigation focused on five key species that breed here: the Spot-billed Pelican, Painted Stork, Black-crowned Night Heron (*Nycticorax nycticorax*), Little Egret (*Egretta garzetta*), and Little Cormorant (*Microcarbo niger*).

To monitor nest fate, systematic ground-based surveys of the entire heronry were conducted at 3–4 day intervals throughout each breeding season (October–August). Observations were made from predefined vantage points and open areas beneath nesting trees to minimize disturbance to breeding birds via Nikon Aculon A211 binoculars (10–22 × 50X). For each nesting tree, we prepared detailed nest maps that served as the primary framework for tracking individual nests from the nest-building stage through fledging or failure. *Nest maps* were constructed by sketching the canopy outline of each tree, incorporating its overall structure, cardinal orientation, and the position of major primary branches, each of which was marked and numbered. Nests were plotted on these maps according to their precise spatial position within the canopy. Species identity was indicated using distinct symbols (e.g., ‘+’ for Spot-billed Pelican nests and ‘*’ for Painted Stork nests), allowing multiple species nesting on the same tree to be tracked simultaneously. Each nest was assigned a unique identification number, enabling consistent monitoring of nest status across successive surveys.

Nest fate was assessed following standard Mayfield criteria (Mayfield, 1975), whereby a nest was classified as successful if it produced at least one fledgling. For analytical purposes, nest outcome was coded as a binary response variable (‘0’ = successful; ‘1’ = failed). Over the five-year study period, the fate of 6,866 nests was successfully monitored, comprising Spot-billed Pelican (n = 942), Painted Stork (n = 4,096), Black-crowned Night Heron (n = 1,258), Little Egret (n = 207), and Little Cormorant (n = 283).

To identify factors influencing nesting success, we compiled a comprehensive set of predictor variables for each nest, grouped into tree- and nest-site characteristics, colony-level metrics, landscape variables, and environmental conditions. For every nesting tree, species identity was determined through direct field observation, and Girth at Breast Height (GBH) was measured using a standard measuring tape. Tree height and nest height were estimated with a 20-ft marked pole, while the distance to the nearest active nest (nearest-neighbor distance) was measured using a shorter 2-ft marked pole. During each census, we recorded the total number of nests present on each tree. In the case of Spot-billed Pelicans, where individuals often construct nests in close proximity forming a single shared platform, we additionally quantified *cluster size*, defined as the number of nests within a single nesting platform. Cluster sizes ranged from two to six nests. The overall canopy/colony area was estimated using satellite imagery and the polygon ruler tool in Google Earth Pro. A colony was defined as a group of nesting trees with overlapping or contiguous canopies, forming a single spatially connected nesting unit.

To characterize the surrounding landscape, the geographic location of each nesting tree was recorded using a handheld GPS unit (Garmin 72; ± 3 m accuracy). These coordinates were used to calculate the nearest distance to built-up areas and roads using ArcGIS and Google Earth Pro. Environmental variables were derived from daily weather data obtained from the Karnataka State Natural Disaster Monitoring Centre, where hourly records were pooled to generate 24-hour summaries of mean, minimum, and maximum temperature, as well as total precipitation. These daily weather metrics were matched to the corresponding nest observation dates.

All statistical analyses were carried out in R version 4.5.1 (R Core Team, 2024). To identify the factors influencing nest success, we used Generalized Linear Mixed Models (GLMMs)

with a binomial error distribution and a logit link function. These models were built using the `glmer()` function from the `lme4` package (Bates *et al.* 2015).

We developed separate models for each of the five species. The predictor variables were chosen based on established ecological theories about the costs and benefits of colonial breeding (Wittenberger and Hunt, 1985). These variables included: temporal factors (nest start date, year), environmental conditions (temperature, precipitation), nest-site characteristics (nest height, nearest neighbor distance), colony metrics (cluster size/nest density, colony area), and landscape features (distance to built-up areas and roads). To account for natural year-to-year variations in breeding conditions, we included Year as a random intercept in all our models (Dinsmore *et al.* 2002).

Before building the models, we checked for multicollinearity among our predictor variables using Pearson's correlation coefficient. To make the effect sizes comparable across different variables and to help the models converge, we standardized all continuous predictors (z-transformed) using the `scale()` function in R.

Our model selection process began with a global model that included all the potential predictors for each species. We then generated all possible subsets of this global model using the `dredge()` function from the `MuMIn` package (Bartoń, 2022). The best-fit model for each species was chosen based on the lowest Akaike Information Criterion (AIC) value. We considered predictors in the final model to be statistically significant if their p-value was less than 0.05.

5.3 Results

Our analysis of 6,866 nests across five waterbird species revealed that a complex combination of temporal, climatic, and spatial factors determines whether a nest succeeds or fails. A summary of annual reproductive outcomes is provided in Table 5. 1. The data reveal

considerable inter-annual variation in nesting success for all species, with success rates fluctuating significantly from one year to the next.

Table 5. 1. Inter-annual variation in nesting success, fledgling production, and stage-specific nest failure of five colonial waterbird species at Kokkare-Bellur (2018–2023). NF stages indicate the developmental stage at which nest failure occurred: Stage 1 = nest building, Stage 2 = incubation, Stage 3 = young chick mortality, Stage 4 = old chick mortality.

Species & Year	Total Nests	Nest Success (%)	Total Fledglings	Total Nest Failures (NF)	NF Stage 1	NF Stage 2	NF Stage 3	NF Stage 4
Spot-billed Pelican								
2018-19	300	21.6	110	235	28	138	63	6
2019-20	219	27.8	91	158	13	90	53	2
2020-21	120	53.3	80	56	9	32	15	0
2021-22	134	42.5	62	77	7	12	33	25
2022-23	169	43.7	87	95	12	38	43	2
Painted Stork								
2019	859	77.7	1245	191	19	74	81	17
2020	926	62.3	1056	349	35	105	194	15
2021	731	85.9	1125	103	21	40	20	22
2022	696	45.4	562	380	16	232	95	37
2023	884	83.4	1284	145	33	45	47	20

Species & Year	Total Nests	Nest Success (%)	Total Fledglings	Total Nest Failures (NF)	NF Stage 1	NF Stage 2	NF Stage 3	NF Stage 4
Black-crowned Night Heron								
2020	559	51.6	384	270	0	145	57	68
2021	301	58.8	242	124	25	46	8	45
2022	210	43.8	147	118	6	83	14	15
2023	188	60.6	178	74	35	28	2	9
Little Egret								
2020	91	35.1	57	59	20	12	7	20
2021	46	68.8	55	15	9	4	0	2
2022	39	43.5	31	22	6	11	4	1
2023	31	48.3	30	16	9	0	1	6
Little Cormorant								
2020	213	41.3	145	125	22	65	29	9
2021	47	55.3	45	21	14	4	0	3
2022	23	52.1	24	11	5	4	0	2

The timing of nesting (nest start day) and the amount of precipitation were the most consistent and powerful predictors across almost all species. The most influential models explaining nest success for each species are summarized in Table 5. 2.

Table 5. 2. Summary of best-fit GLMM models predicting nesting failure for five colonial waterbird species at Kokkare-Bellur. All models include 'Year' as a random intercept. This table shows only the statistically significant predictors ($p < 0.05$) and their estimated effects.

Species (n)	Significant Predictors	Estimate
Spot-billed Pelican (942)	Cluster Size	-0.46
	Nest Density	-0.55
	Nest Height	0.47
	Nest Start Day	-0.24
	Total Precipitation	-1.48
Painted Stork (4,096)	Nest Start Day	4.66
	Minimum Temperature	-3.05
	Total Precipitation	-7.16
Black-crowned Night Heron (1,258)	Colony Area	-0.18
	Nearest Distance to Built-up Area	0.13
	Nest Density	-0.58
	Nest Start Day	2.00
	Minimum Temperature	0.19
	Total Precipitation	-2.71
Little Egret (207)	Nest Start Day	3.65
	Total Precipitation	-4.99
Little Cormorant (283)	Nest Start Day	3.60
	Colony Area	-0.88
	Total Precipitation	-4.50

The best-fit model for Spot-billed Pelican nest survival retained cluster size, nest density, nest height, nest start day, and total precipitation as significant predictors (Table 5.3). The probability of nest failure was negatively associated with cluster size (Estimate = -0.46, $p < 0.001$), nest density (Estimate = -0.55, $p < 0.001$), and total precipitation (Estimate = -1.49, $p < 0.001$). Nest height had a significant positive association with nest failure (Estimate = 0.47, $p < 0.001$). Nest start day showed a weak negative association with nest failure (Estimate = -0.24, $p = 0.049$), indicating a slight decrease in failure probability for nests initiated later in the season (Fig. 5.1).

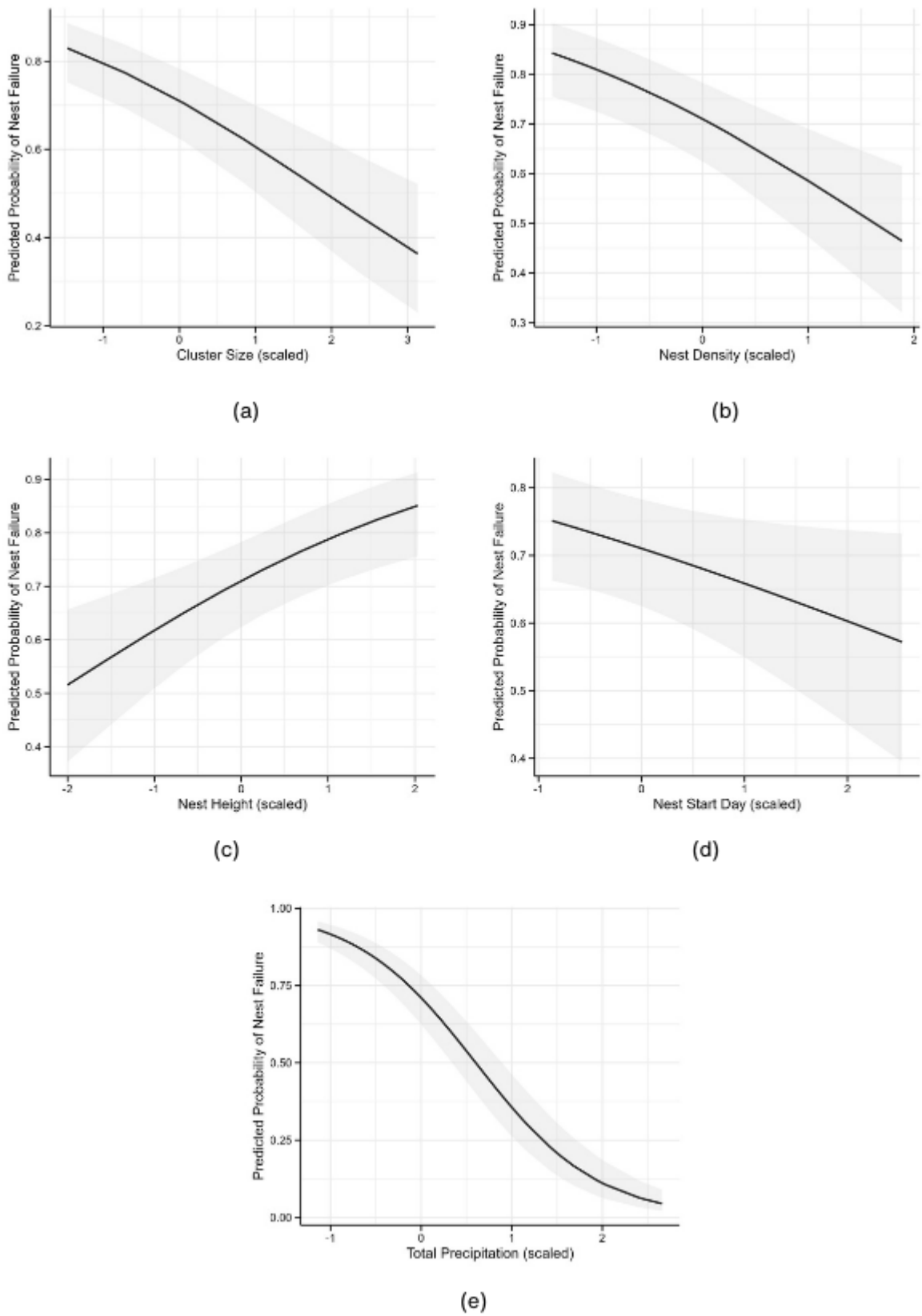


Figure 5.1. Model-predicted effects of ecological, temporal, and climatic variables on nest failure probability in Spot-billed Pelicans. Panels show the predicted probability of nest

failure as a function of (a) cluster size, (b) nest density, (c) nest height, (d) nest initiation date, and (e) total precipitation. Shaded bands represent 95% confidence intervals.

Table 5.3. AICc-based model selection evaluating temporal, climatic, nest-site, anthropogenic, and colony-level predictors of nest failure in Spot-billed Pelican. The full model included nest initiation timing, climatic variables (minimum temperature and total precipitation), nest-site characteristics (nest height, nearest-neighbor distance, nest density, and cluster size), anthropogenic proximity (distance to road and distance to built-up area), and colony area.

Model	Predictor combination	AICc	ΔAICc
Full model	Nest start day + Minimum temperature + Total precipitation + Nest height + Nearest-neighbor distance + Nest density + Cluster size + Distance to road + Distance to built-up area + Colony area	881.44	6.61
Best model	Nest start day + Total precipitation + Nest height + Nest density + Cluster size	874.83	0.00
1	Nest start day + Cluster size + Distance to road + Distance to built-up area + Colony area	874.95	0.12
2	Nest start day + Nearest-neighbor distance + Cluster size + Distance to road + Distance to built-up area + Colony area	875.47	0.64
3	Nest start day + Total precipitation + Cluster size + Distance to road + Colony area	876.13	1.30
4	Nest start day + Nest density + Cluster size + Distance to road + Distance to built-up area + Colony area	876.43	1.60

Model	Predictor combination	AICc	ΔAICc
5	Nest start day + Nest height + Cluster size + Distance to road + Distance to built-up area + Colony area	876.58	1.75
6	Nest start day + Total precipitation + Nearest-neighbor distance + Cluster size + Distance to road + Colony area	876.64	1.81
7	Nest start day + Nearest-neighbor distance + Cluster size + Distance to road + Colony area	876.91	2.08
8	Nest start day + Nearest-neighbor distance + Nest density + Cluster size + Distance to road + Distance to built-up area + Colony area	876.91	2.08
9	Nest start day + Cluster size + Distance to road + Colony area	876.91	2.08
10	Nest start day + Minimum temperature + Cluster size + Distance to road + Distance to built-up area + Colony area	876.93	2.10

Nest survival for Painted Storks was most strongly predicted by nest start day, minimum temperature, and total precipitation (Table 5.4). A strong positive relationship was found between nest start day and failure probability (Estimate = 4.63, $p < 0.001$). Conversely, both minimum temperature (Estimate = -2.97, $p < 0.001$) and total precipitation (Estimate = -7.15, $p < 0.001$) had strong negative relationships with nest failure. Canopy area was retained in the top model set but was not a significant predictor ($p = 0.13$). The random effect for year was substantial ($\sigma^2 = 7.47$), indicating strong inter-annual variation in survival (Fig. 5.2).

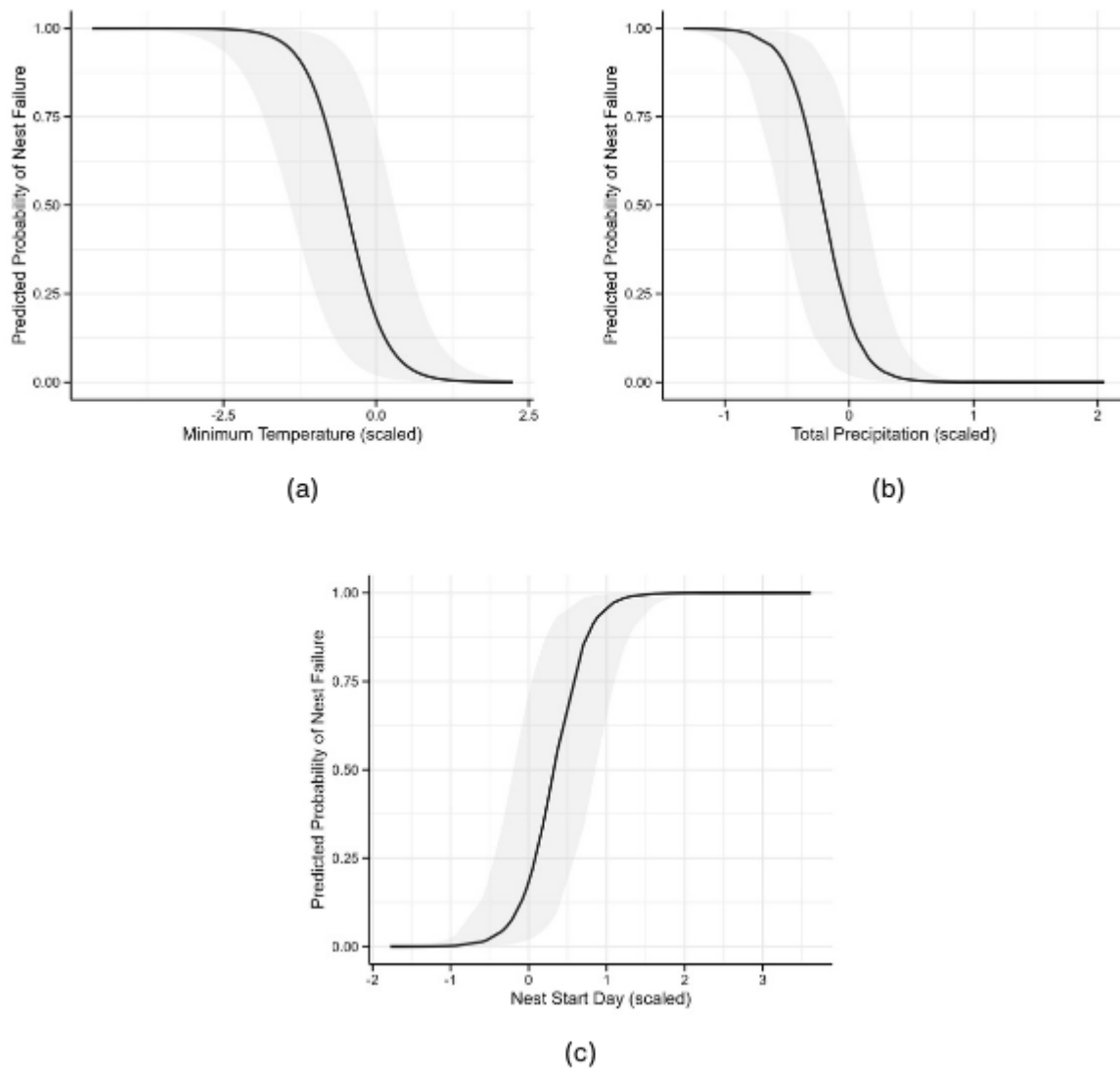


Figure 5.2. Model-predicted effects of climatic and phenological variables on nest failure probability in Painted Storks. Panels show predicted probabilities as a function of (a) minimum **temperature**, (b) total precipitation, and (c) nest initiation date based on the best-supported model. Shaded bands represent 95% confidence intervals.

Table 5.4. AICc-based model selection identifying key determinants of nest failure in Painted Stork.

Candidate models assessed the influence of nest initiation timing, climatic conditions (minimum temperature and total precipitation), nest-site attributes (nest height, nearest-

neighbor distance, and nest density), anthropogenic proximity, and canopy area.

Models within $\Delta AICc \leq 2$ are considered to have substantial empirical support.

Model	Predictor combination	AICc	$\Delta AICc$
Full model	Nest start day + Minimum temperature + Total precipitation + Nest height + Nearest-neighbor distance + Nest density + Distance to road + Distance to built-up area + Canopy area	549.05	7.36
Best model	Canopy area + Minimum temperature + Nest start day + Total precipitation	541.69	0.00
1	Canopy area + Minimum temperature + Nest start day + Total precipitation	541.70	0.01
2	Canopy area + Minimum temperature + Nest density + Nest start day + Total precipitation	541.91	0.22
3	Minimum temperature + Nest density + Nest start day + Total precipitation	542.00	0.31
4	Minimum temperature + Nest start day + Total precipitation	542.03	0.34
5	Canopy area + Minimum temperature + Nest height + Nest start day + Total precipitation	543.11	1.42
6	Minimum temperature + Nearest-neighbor distance + Nest density + Nest start day + Total precipitation	543.24	1.55
7	Canopy area + Minimum temperature + Nest density + Nest height + Nest start day + Total precipitation	543.29	1.60
8	Canopy area + Minimum temperature + Nest density + Nest start day + Total precipitation	543.43	1.74

Model	Predictor combination	AICc	ΔAICc
9	Canopy area + Minimum temperature + Nearest-neighbor distance + Nest start day + Total precipitation	543.60	1.91
10	Canopy area + Minimum temperature + Distance to road + Nest start day + Total precipitation	543.69	2.00

The model-averaged results for Black-crowned Night Heron showed that nest survival was influenced by a combination of landscape, colonial, temporal, and climatic variables (Table 5.5). The probability of nest failure decreased significantly with increasing colony area (Estimate = -0.18, $p = 0.010$) and nest density (Estimate = -0.59, $p < 0.001$). Later nest initiation (Estimate = 2.00, $p < 0.001$) and higher minimum temperatures (Estimate = 0.19, $p = 0.016$) were positively associated with failure. Total precipitation showed a strong negative association with failure (Estimate = -2.71, $p < 0.001$). Distance to built-up areas showed a weak, positive association with failure that was of borderline significance ($p = 0.056$) (Fig. 5.3).

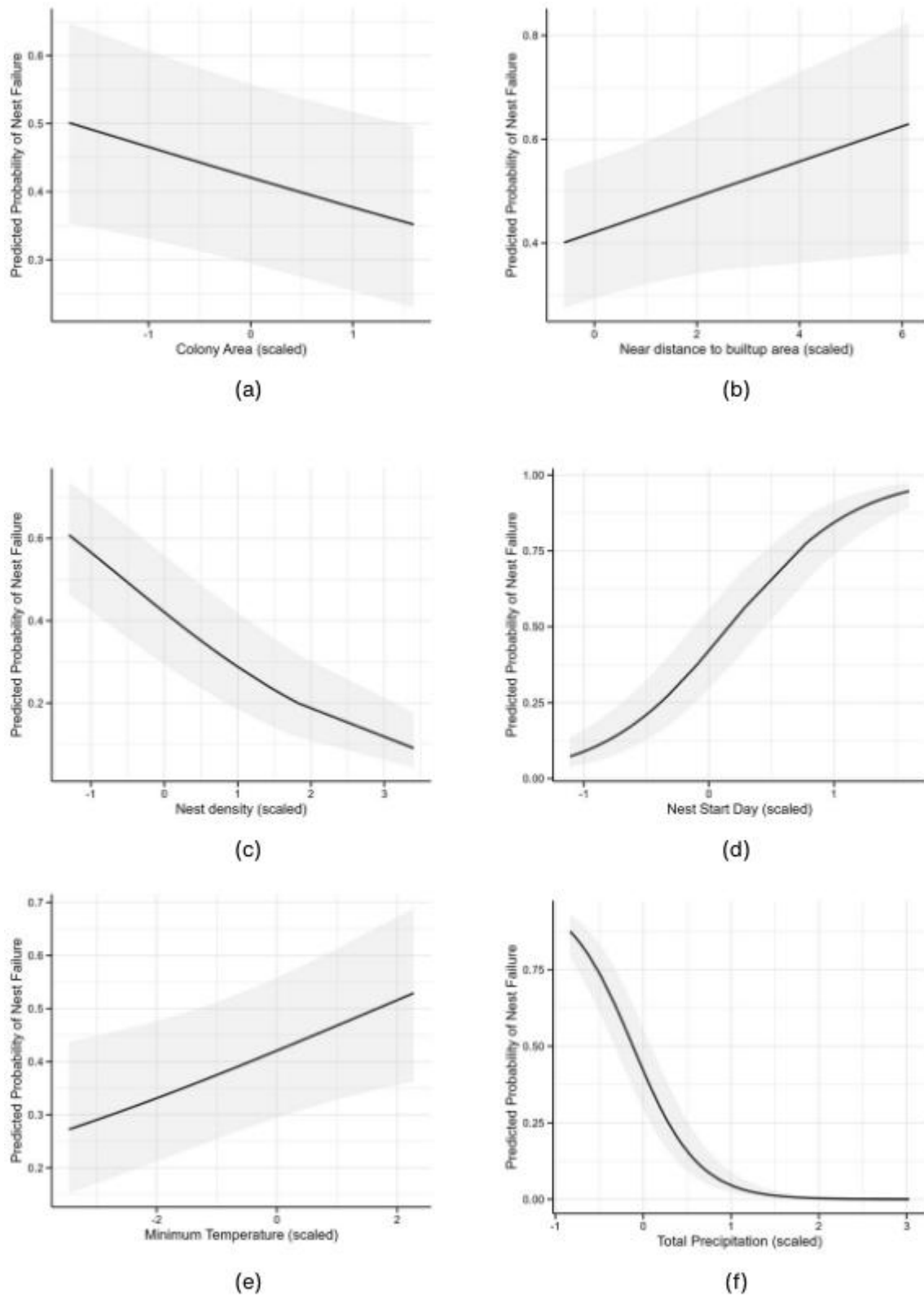


Figure 5.3. Model-predicted effects of colony structure, landscape context, nesting phenology, and climatic variables on nest failure probability in Black-crowned Night Herons. Panels show predicted probabilities as a function of (a) colony area, (b) distance to

built-up areas, (c) nest density, (d) nest initiation date, (e) minimum temperature, and (f) total precipitation based on the best-supported model. Shaded bands represent 95% confidence intervals.

Table 5.5 Model selection results for predictors influencing nest failure in Black-crowned Night Heron using AICc. Models evaluated the relative importance of temporal, climatic, nest-site, anthropogenic, and colony-level variables, including nest initiation timing, temperature, precipitation, nest density, proximity to built-up areas, and colony area. Lower AICc values indicate better-supported models.

Model	Predictor combination	AICc	ΔAICc
Full model	Nest start day + Minimum temperature + Total precipitation + Nest height + Nearest-neighbor distance + Nest density + Distance to road + Distance to built-up area + Colony area	1358.58	4.74
Best model	Colony area + Minimum temperature + Distance to built-up area + Nest density + Nest start day + Total precipitation	1353.85	0.00
1	Colony area + Minimum temperature + Distance to built-up area + Nest density + Nest start day + Total precipitation	1353.96	0.11
2	Colony area + Minimum temperature + Distance to built-up area + Nest density + Nest height + Nest start day + Total precipitation	1355.09	1.24
3	Colony area + Minimum temperature + Distance to built-up area + Nest density + Nest start day + Total precipitation + Nearest-neighbor distance	1355.42	1.57
4	Colony area + Minimum temperature + Nest density + Nest start day + Total precipitation	1355.66	1.81

Model	Predictor combination	AICc	Δ AICc
5	Colony area + Minimum temperature + Distance to built-up area + Nest density + Nest start day + Total precipitation + Nest height	1355.80	1.95

For Little Egret, the best-fit model identified only nest start day and total precipitation as significant predictors (Table 5.6). Nest start day had a strong positive relationship with the probability of failure (Estimate = 3.65, $p < 0.001$). Total precipitation had a strong negative relationship with failure probability (Estimate = -4.99, $p < 0.001$). Other variables, including distance to road and nearest neighbor distance, were retained in the top model set but were not statistically significant ($p > 0.05$) (Fig. 5.4).

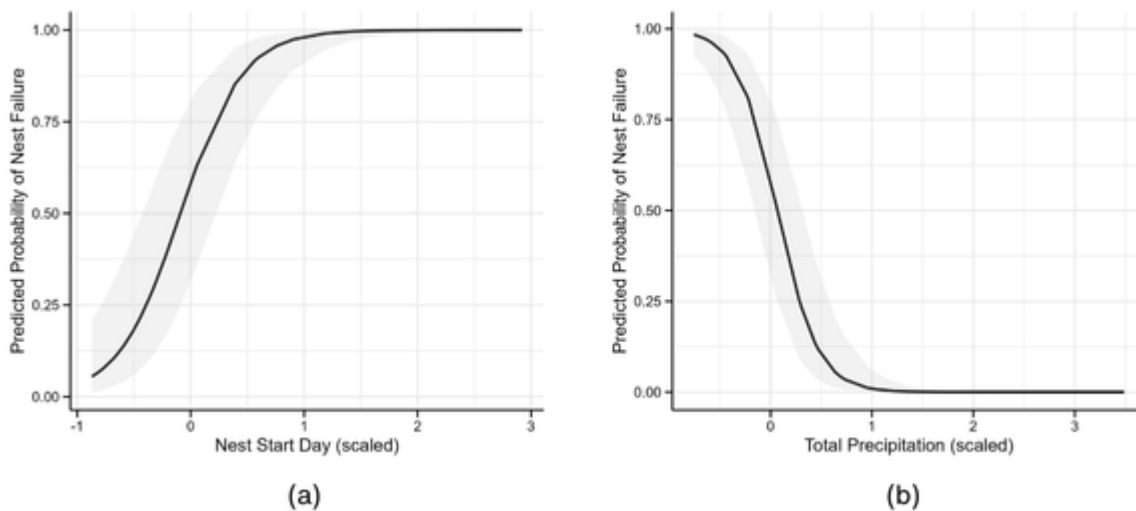


Figure 5.4. Model-predicted effects of nesting phenology, and climatic variables on nest failure probability in Little Egret. Panels show predicted probabilities as a function of (a) nest initiation date, and (b) total precipitation based on the best-supported model. Shaded bands represent 95% confidence intervals.

Table 5.6 AICc-based model selection assessing factors affecting nest failure in Little Egret.

Candidate models examined the effects of nest initiation timing, climatic variables, nest-site characteristics, anthropogenic proximity, and colony area. Predictor combinations are ranked according to AICc, with Δ AICc reflecting relative model support.

Model	Predictor combination	AICc	ΔAICc
Full model	Nest start day + Minimum temperature + Total precipitation + Nest height + Nearest-neighbor distance + Nest density + Distance to road + Distance to built-up area + Colony area	170.73	7.24
Best model	Distance to road + Nearest-neighbor distance + Nest start day + Total precipitation	163.49	0.00
1	Distance to road + Nearest-neighbor distance + Nest start day + Total precipitation	163.91	0.42
2	Distance to road + Nest start day + Total precipitation	164.02	0.53
3	Nearest-neighbor distance + Nest start day + Total precipitation	164.13	0.64
4	Nest start day + Total precipitation	164.24	0.75
5	Nest start day + Total precipitation + Distance to built-up area	164.29	0.80
6	Distance to road + Nearest-neighbor distance + Nest start day + Total precipitation + Nest density	164.97	1.48
7	Nest start day + Total precipitation + Nest height	165.07	1.58
8	Distance to road + Nearest-neighbor distance + Nest start day + Total precipitation + Distance to built-up area	165.24	1.75
9	Distance to road + Nearest-neighbor distance + Nest start day + Total precipitation + Colony area	165.37	1.88

Model	Predictor combination	AICc	Δ AICc
10	Distance to road + Nearest-neighbor distance + Nest start day + Total precipitation + Minimum temperature	165.56	2.07

The best-fit model for the Little Cormorant, a GLM used due to a singular fit in the mixed-effects model, retained colony area, nest start day, and total precipitation as predictors (Table 5.7). The probability of nest failure was negatively associated with colony area (Estimate = -0.88, $p < 0.001$) and total precipitation (Estimate = -4.50, $p < 0.001$). Nest start day showed a strong positive association with nest failure (Estimate = 3.60, $p < 0.001$) (Fig. 5.5).

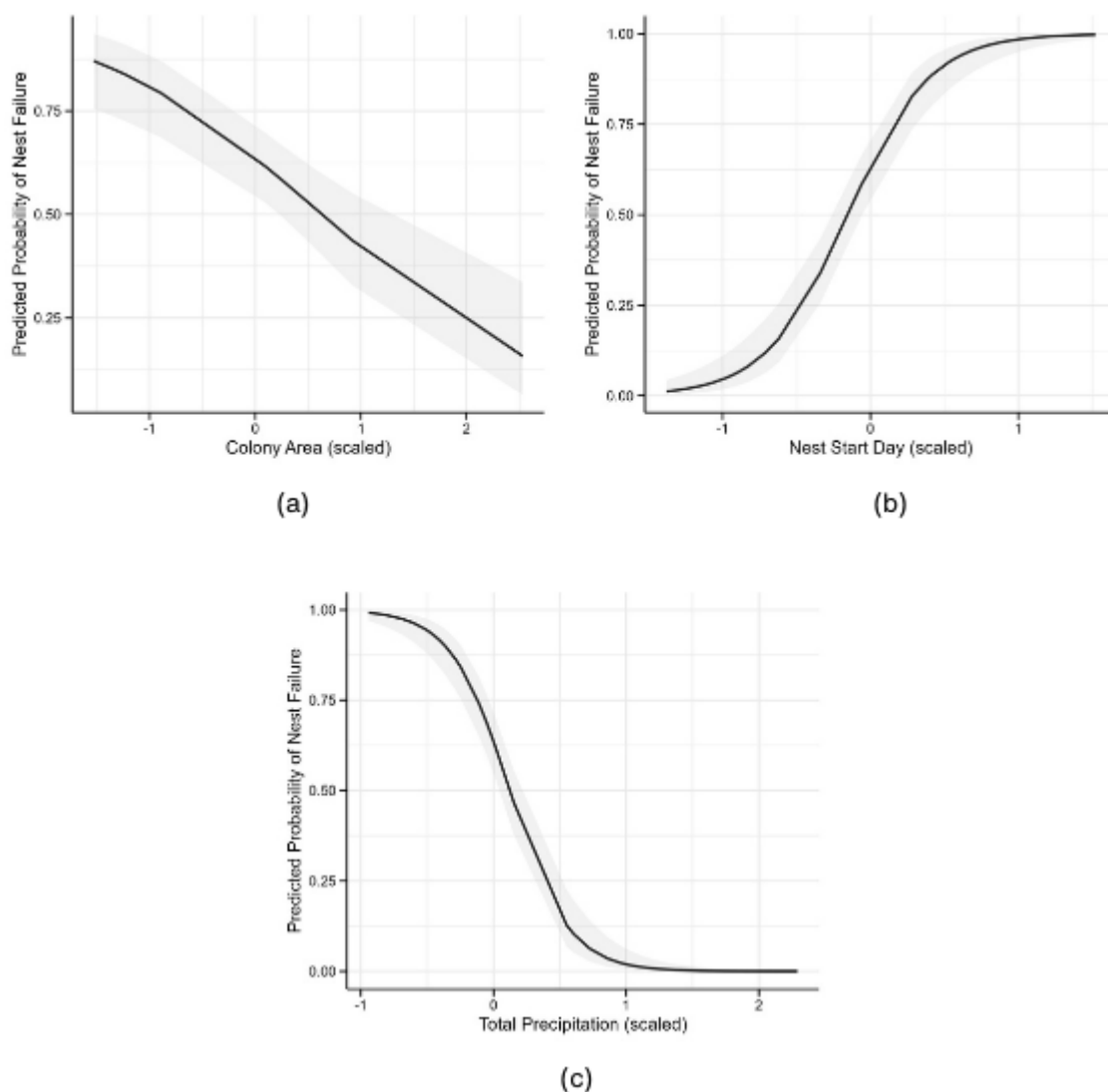


Figure 5.5. Model-predicted effects of colony structure, nesting phenology, and climatic variables on nest failure probability in Little Cormorant. Panels show predicted probabilities as a **function** of (a) colony area, (b) nest initiation date, and (c) total precipitation based on the best-supported model. Shaded bands represent 95% confidence intervals.

Table 5.7 AICc-based model selection evaluating drivers of nest fate in Little Cormorant. Models assessed the influence of temporal (nest start day), climatic (minimum temperature and total precipitation), nest-site, anthropogenic, and colony-level variables. The best-supported models highlight the relative contribution of colony area and climatic timing effects on nesting outcomes.

Model type	Predictors included	AICc	ΔAICc
Full model	Nest start day + minimum temperature + total precipitation + nest height + neighbour distance + nest density + distance to road + distance to built-up area + colony area	228.10	8.23
Best model	Colony area + nest start day + total precipitation	219.87	0.00
1	Colony area + minimum temperature + nest start day + total precipitation	221.29	1.28
2	Colony area + nest density + nest start day + total precipitation	221.39	1.38
3	Colony area + nest height + nest start day + total precipitation	221.64	1.63
4	Colony area + distance to built-up area + nest start day + total precipitation	221.98	1.97

5. 4 Discussion

This study demonstrates that reproductive success in a multi-species colonial waterbird assemblage nesting within an anthropogenic landscape is shaped by a hierarchical interaction of breeding phenology, monsoon-driven environmental conditions, and species-specific social and spatial strategies. While several of the patterns observed here are consistent with established theory on avian coloniality and reproductive timing, the strength and direction of these effects vary markedly among species, reflecting divergent life-history traits and ecological niches. Importantly, our results show that in an inland, rain-shadow system such as Kokkare-Bellur, climatic variability particularly precipitation acts as a dominant ecological filter through which other determinants of nesting success operate. Nest initiation timing emerged as one of the most influential predictors of nesting success across species, underscoring the central role of phenology in colonial waterbirds. For Painted Storks, Black-crowned Night Herons, Little Egrets, and Little Cormorants, later nest initiation was associated with sharply increased failure probabilities, indicating that reproductive success is constrained within a relatively narrow temporal window. Such phenology-driven variation in nest survival is well documented in ardeids and other wading birds, where asynchronous nesting results in successive cohorts experiencing markedly different environmental conditions (Lack, 1968; McCreedy and Riper, 2015; Tiwary and Urfi, 2016). Early-season breeders are likely to benefit from a combination of favorable weather conditions, reduced competition for nesting space, and improved alignment between peak nestling energetic demands and seasonal prey availability. Moreover, early breeders may represent individuals in superior physiological condition, as suggested by previous work on Painted Storks showing that early-mating birds tend to be larger-bodied and presumably of higher quality (Urfi, 2011). Consequently, early nests may contain older, more developmentally advanced nestlings at times later in the season

when environmental conditions deteriorate, reducing their vulnerability to hypothermia, starvation, or predation. In contrast, nestlings from late-initiated nests may be at early developmental stages during periods of adverse weather, when they lack sufficient plumage or thermoregulatory capacity, thereby increasing failure risk (Taff and Shipley, 2023). The Spot-billed Pelican presented a notable exception to this trend, exhibiting higher reproductive success with later nest initiation. At Kokkare-Bellur, pelicans are the earliest arriving breeders, initiating nesting as early as October, coinciding with the transition between the southwest and northeast monsoons (Shilpashree *et al.* 2016). Painted Storks typically arrive later, followed by smaller-bodied waterbirds in subsequent months, creating a temporally structured breeding assemblage. For pelicans, delayed nesting may confer advantages linked to local hydrology and prey dynamics. As large-bodied pursuit foragers, pelicans may benefit disproportionately from receding water levels later in the season, when fish become concentrated in shrinking wetlands, irrigation tanks, and agricultural channels (Frederick and Loftus, 1993). Additionally, early-season nests may be more exposed to climatic instability during the monsoon transition period, whereas later nests experience relatively stable conditions. This pattern suggests temporal niche differentiation within the colony, potentially reducing interspecific competition with the numerically dominant Painted Stork and allowing coexistence through staggered reproductive strategies.

Precipitation was the most consistent and powerful predictor of nesting success across all five species, with increased precipitation strongly reducing nest failure probabilities. This finding is particularly significant given the location of Kokkare-Bellur in the rain-shadow region of the Western Ghats, where annual precipitation is relatively low (mean 750 ± 207 mm) and highly variable (Shilpashree *et al.* 2016). Unlike floodplain or coastal heronries, inland colonies in such landscapes are acutely sensitive to monsoon dynamics, as precipitation directly governs wetland extent, hydroperiod, and prey availability. Contrary to the expectation that heavy

precipitation would be detrimental due to the direct risks of nest failure and chick hypothermia (Arct *et al.* 2025), our models indicated that higher total precipitation was strongly correlated with increased nesting success. This demonstrates the primacy of resource availability over direct climatic stressors in this monsoonal ecosystem. For these predominantly piscivorous species, precipitation functions as the principal driver of a resource pulse, replenishing the surrounding wetland and agricultural mosaic and thereby increasing the productivity and accessibility of aquatic prey (Urfi, 2011; Djerdali *et al.* 2008). The fitness benefits gained from this enhanced parental provisioning capacity appear to substantially outweigh the direct physical costs of inclement weather.

Minimum temperature emerged as a significant predictor of nest failure for some species, particularly Painted Storks and Black-crowned Night Herons. This contrasts with studies from northern India, where extreme winter cold has been linked to hypothermia-induced nestling mortality (Tiwary and Urfi, 2016). At Kokkare-Bellur, however, ambient temperatures rarely fall below 16 °C (Shilpashree *et al.* 2016), suggesting that temperature effects here may operate indirectly through interactions with rainfall, prey availability, or parental energetics rather than through acute thermal stress. The relatively benign thermal regime of southern India may thus buffer nesting waterbirds from the extreme cold-related mortality observed at higher latitudes, reinforcing the importance of comparative studies across climatic zones to fully understand temperature-mediated reproductive constraints.

The social environment of the colony also proved to be a significant factor. For Spot-billed Pelicans, Black-crowned Night Herons, and Little Cormorants, increased nest density or larger colony area was positively correlated with nest survival. This provides empirical support for foundational hypotheses of avian coloniality, which propose that aggregation enhances fitness through mechanisms such as improved anti-predator vigilance, predator dilution effects, and the function of the colony as an information center for locating ephemeral food sources

(Wittenberger and Hunt, 1985; Brown and Brown, 2001). The lack of a uniform effect across all species suggests that the net adaptive value of coloniality is modulated by species-specific vulnerabilities to predation and competition. The positive association between nest height and failure in Spot-billed Pelicans highlights the trade-offs inherent in nest-site selection. While elevated nests may reduce predation risk, they may also be more exposed to wind, thermal stress, or structural instability, particularly under variable weather conditions. Such trade-offs likely differ among species depending on body size, nesting architecture, and parental behavior, contributing to the observed interspecific variation in social effects.

One of the novel insights derived from this study concerns the influence of the anthropogenic landscape. The finding that Black-crowned Night Heron nests located in closer proximity to human-built structures experienced higher success provides evidence for a "human shield" or "predator refuge" hypothesis (Tryjanowski *et al.* 2013). The continuous presence of villagers may create a spatial refuge from natural predators that exhibit greater avoidance of human activity, thereby inadvertently increasing nest survival. This phenomenon challenges the paradigm that human presence is uniformly detrimental to wildlife and underscores the profound conservation value of traditional socio-ecological systems like Kokkare-Bellur, where centuries of cultural protection have fostered positive human-wildlife interactions (Manakadan and Kannan, 2003; Kannan, 2023).

5. 5 Conclusion

In conclusion, this study provides a comprehensive, multi-species assessment of the determinants of waterbird nesting success within a unique, human-inhabited socio-ecological system. Our results demonstrate that reproductive outcomes are governed by species-specific strategies responding to the interplay of breeding phenology, monsoon-driven resource pulses, and the social dynamics of the colony. We provide strong evidence that early nesting and high

precipitation are primary drivers of success for most species, and that colonial nesting confers significant fitness benefits. Critically, we also reveal the potential for positive anthropogenic influence through a predator refuge effect, highlighting the conservation significance of community-protected heronries. These findings not only advance our understanding of colonial waterbird ecology but also affirm the vital role that traditional, community-based conservation models can play in safeguarding threatened species in an increasingly human-dominated world. As global environmental change continues to alter climatic patterns and land use, such long-term studies of culturally protected sites will be indispensable for developing effective, place-based conservation strategies.

Chapter – 6

FORAGING HABITAT DYNAMICS AND RANGING PATTERNS OF SPOT-BILLED PELICAN DURING THE BREEDING AND NON-BREEDING PHASES

6.1 Introduction

Wildlife rescue and rehabilitation are widely applied conservation interventions for injured, orphaned, or displaced birds, yet their effectiveness is rarely evaluated beyond short-term survival (Pyke *et al.* 2018; Hernandez, 2019). In this context, post-release monitoring is a powerful approach for assessing the functional outcomes of rehabilitation, including dispersal behavior, space use, and landscape integration (Bernardo *et al.* 2011; Raine *et al.* 2020; Rozsypalová *et al.* 2025). GPS telemetry studies on rehabilitated pelicans following oil spills have demonstrated altered movement strategies, increased dispersion, and reduced breeding investment relative to non-rehabilitated individuals, highlighting the need for long-term behavioral assessment of released birds (Lamb *et al.* 2018; Fiorello *et al.* 2021).

Pelicans are large, colonial, piscivorous waterbirds that function as top predators in aquatic ecosystems and are widely regarded as indicators of wetland health due to their sensitivity to changes in water quality, fish availability, and disturbance to breeding sites (del Hoyo *et al.* 1992; Amat and Green, 2010). Among the eight extant pelican species, the Spot-billed Pelican (*Pelecanus philippensis*), a tree-nesting species distributed across South and Southeast Asia, remains poorly studied (Kannan and Pandiyan, 2013; BirdLife International, 2017). In India, the species breeds at approximately 20 sites, primarily in southern states, and is classified as Near Threatened due to the loss of wetlands, human disturbance, and emerging disease threats (Kannan and Pandiyan 2013). Despite its conservation importance, empirical information on its current population status, movements are limited, and more specifically survival following rescue or rehabilitation efforts remains unknown.

Kokkare-Bellur Community Reserve represents one of the oldest and important breeding sites for Spot-billed Pelican in southern India. Alarmingly, between 2017 and 2018, this site experienced a mass mortality event involving more than 50 adult pelicans, later attributed to heavy gastrointestinal nematode infestations associated with degraded wetland conditions (Kumar *et al.* 2019). Similar mortality events linked to *Contracaecum* infestations have since been reported from other pelican breeding and foraging sites in southern India (Durairajan, 2023; Mathews *et al.* 2025), underscoring growing concerns regarding adult survival, and exposure to environmental stressors. These events prompted tracking fine-scale movements of rescued pelicans to understand their ranging behavior, wetland use, and evaluate the overall success of rehabilitation efforts.

Here, we present a case report of documenting spatio-temporal movements of two rescued Spot-billed Pelicans, a hand-raised juvenile and a rehabilitated adult, tracked for approximately two years using GPS telemetry following their release from Kokkare-Bellur site. This study offers a rare, detailed look into the individual-level movement ecology of this species, providing valuable data for future conservation and reintroduction programs.

Research Objectives and Hypotheses

Research Objective:

The primary objective of this study is to examine foraging habitat use and ranging patterns of the Spot-billed Pelican (*Pelecanus philippensis*) during breeding and non-breeding phases at Kokkare-Bellur, Southern India, in order to understand seasonal shifts in space use and habitat requirements.

a) What are the key foraging habitats utilized by Spot-billed Pelicans during the breeding and non-breeding phases?

b) How do the ranging patterns of Spot-billed Pelicans differ between breeding and non-breeding phases in terms of spatial extent and movement behavior?

Hypothesis:

Foraging habitat use and ranging patterns of Spot-billed Pelicans vary significantly between breeding and non-breeding phases in response to changing energetic demands, breeding constraints, and seasonal variation in resource availability. It is hypothesized that during the breeding phase, pelicans will exhibit more restricted ranging patterns and higher reliance on nearby wetlands and predictable foraging sites to meet the demands of incubation and chick provisioning. In contrast, during the non-breeding phase, pelicans are expected to use a broader range of foraging habitats and exhibit expanded movement ranges, reflecting reduced central-place foraging constraints and greater flexibility in habitat selection. Understanding these seasonal dynamics will contribute to improved identification of critical foraging habitats and support the development of targeted conservation and management strategies for the Spot-billed Pelican and other colonial waterbirds in human-dominated landscapes.

6. 2 Methods

This study was conducted as part of a five-year monitoring programme of Spot-billed Pelican breeding ecology at Kokkare-Bellur Community Reserve, Karnataka. The site exemplifies a unique conservation model, wherein colonial waterbirds, primarily Spot-billed Pelicans and Painted Storks *Mycteria leucocephala*, nest within a human-inhabited village landscape. Nesting trees are distributed in scattered patches throughout residential areas, agricultural lands, and temple grounds rather than in an isolated tree patch in a wetland.

During monitoring, natural falls of pelican chicks and adults from nests were documented, attributed to sibling competition, adverse weather, fledging attempts, and illness. During the

2022–23 breeding season, a total of 13 chicks and two adults were rescued and rehabilitated, of which two individuals were selected for GPS tagging based on health status and growth parameters. A chick rescued at four days old on 16 January 2022 was hand-raised and released on 9 November 2022 (named Shimsha; body mass at tagging = 4865 g), while an adult pelican rescued in a dehydrated condition on 21 December 2022 received veterinary treatment and was released on 4 February 2023 (named Aadi; body mass at tagging = 4480g). Both pelicans were released near the village in proximity to the Shimsha River and were fitted with 33 g solar-powered GPS-GSM patagial transmitters (OrniTrack P33, Ornitela, Lithuania). Transmitters were programmed to record GPS locations at 10-minute intervals with daily data transmission. Movement data were obtained from September 10, 2022, to August 31, 2024, for Shimsha (722 days) and from February 4, 2023, to February 28, 2025, for Aadi (755 days). For Shimsha, GPS data collection ended prematurely on August 31, 2024, after the transmitter detached and fell into the river; however, subsequent field observations confirmed that the bird retained the patagial tag and was repeatedly recorded flying, foraging, and hunting fish, indicating normal movement and an apparently healthy condition.

For Shimsha, the data were partitioned into Year 1 (November 9, 2022, to November 9, 2023) and Year 2 (November 10, 2023, to August 31, 2024). The data was treated separately for each year to quantify annual changes in space use. For Aadi, data were partitioned into breeding and non-breeding seasons across two cycles. Breeding seasons were defined as October 2023 to April 2024 (Year 1) and October 2024 to February 2025 (Year 2) based on observed nesting activity and colony monitoring. Non-breeding seasons comprised the remaining months.

Data processing was conducted in R version 4.3.1 (R Core Team 2024) using packages *move* (Kranstauber *et al.* 2024), *raster* (Hijmans *et al.* 2025), *sp*, (Pebesma *et al.* 2025) and *sf* (Pebesma *et al.* 2025). The daily distance traveled was calculated by summing the distances between consecutive locations within each 24-hour period. The daily distance data was

summarized using median and range. For a visual representation, the daily distance was plotted using a LOESS regression.

To quantify space use and identify core areas, we employed Dynamic Brownian Bridge Movement Model (dBBMM), which estimate an animal's probability of occurrence by incorporating the time and distance between consecutive locations and the animal's movement variance (Kranstauber *et al.* 2012). The dBBMM was computed using the `brownian.bridge.dyn` function in the package 'move' with a window size of 31 and a margin of 11 fixes to capture temporal variations in movement behavior. A location error of 20 m was specified, and a high-resolution grid (`dimSize = 600`) was used to ensure detailed contouring. From the resulting Utilization Distribution (UD) raster, we extracted isopleths for the 50% (core use area), 75% (primary use area), and 99% (overall utilization distribution) contours to quantify annual and seasonal differences in space use for each individual. Seasonal dBBMMs enabled the quantification of reproductive versus non-reproductive space-use patterns. Spatial outputs were visualized in QGIS 3.28, utilizing satellite imagery, to identify core wetlands and map movement patterns.

6. 3 Results

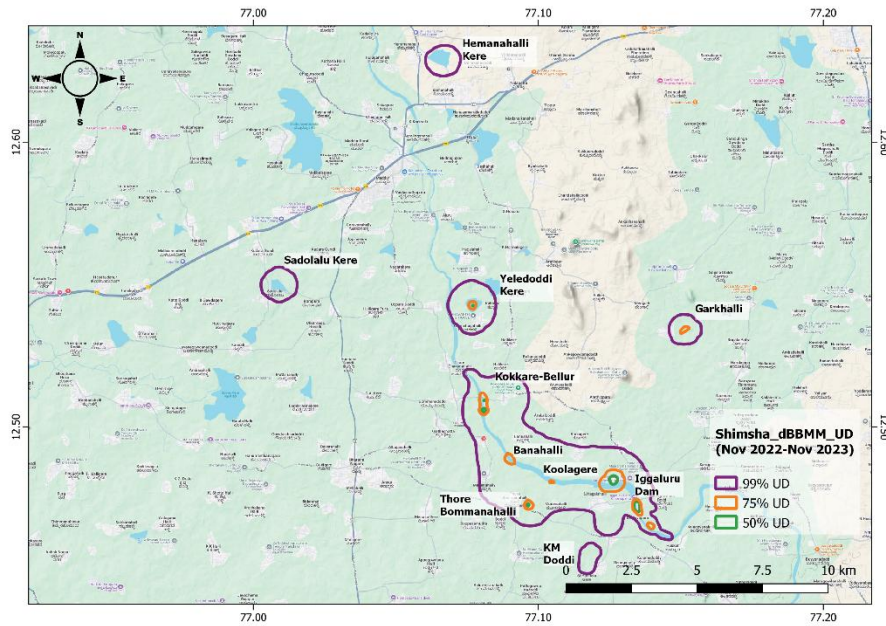
Juvenile pelican (Shimsha) movement patterns

Shimsha was tracked for 723 days post-release, generating 104,112 GPS locations. Movement patterns were predominantly concentrated around the release location along the Shimsha River, with opportunistic exploratory movements to neighboring inland wetlands. A single long-distance movement to Mysuru (approximately 80 km from release site) was also recorded, during which Shimsha visited multiple wetlands before returning to the core area.

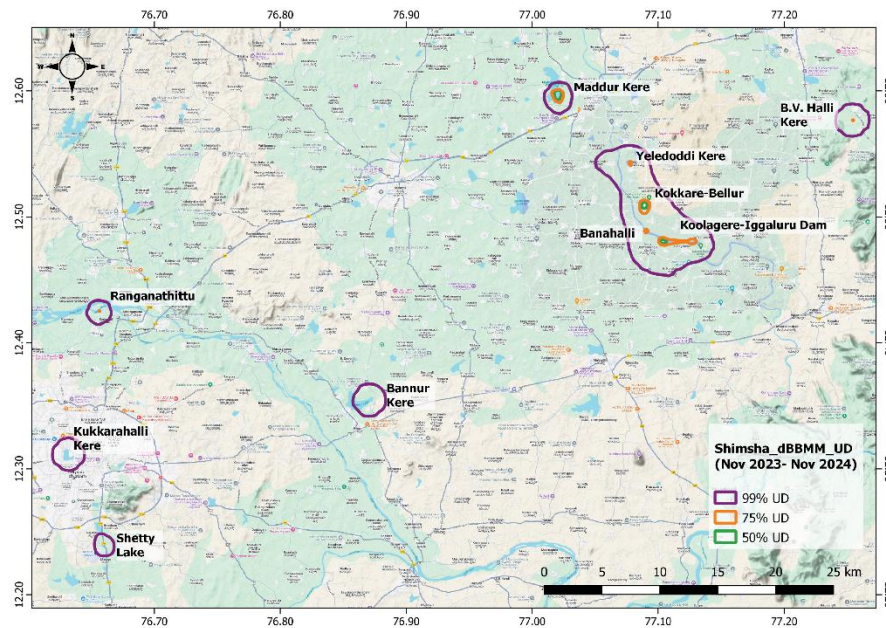
During the first year (November 2022 to November 2023), Shimsha's movements remained highly localized. The 50% core utilization area was very small (less than 1 sq. km). The 75%

UD encompassed 1 sq. km, whilst the 99% UD extended to 32 sq. km, capturing the full extent of exploratory movements along sections of the Shimsha River within 10 km of the release location and two neighboring lakes.

In the second year (November 2023 to November 2024), Shimsha's core areas shifted spatially and expanded substantially. The 50% UD covered 1 sq. km, encompassing sections of the Shimsha River and more distant lakes, including Maddur Lake and BV Halli Kere, located farther from the release location. Relative to the first year, the 75% UD expanded to 3 sq. km (a 200% increase from Year 1), while the 99% UD showed the most substantial expansion, reaching 86 sq. km (a 169% increase), reflecting increased ranging behavior and the utilization of more distant wetland networks (Fig. 6.1).



(a)



(b)

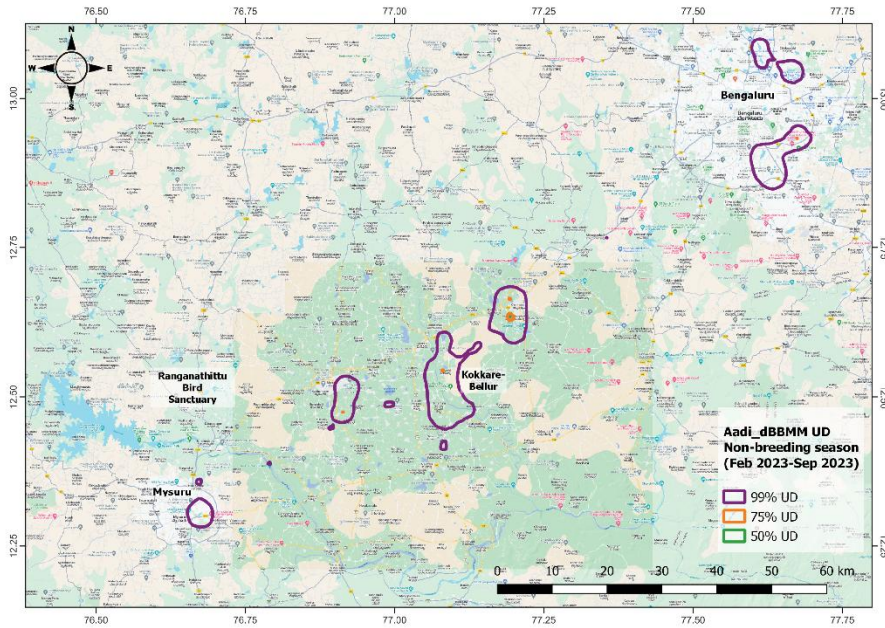
Figure 6.1. Utilization distributions (UD) of the juvenile Spot-billed Pelican (Shimsha) derived from Dynamic Brownian Bridge Movement Models (dBBMM). The maps show the 50% (core), 75% (primary), and 99% (overall) UD for (a) the first-year post-release (November 2022–November 2023) and (b) the second-year post-release (November

2023–November 2024), illustrating spatial expansion over time. Note that both maps are on independent scales.

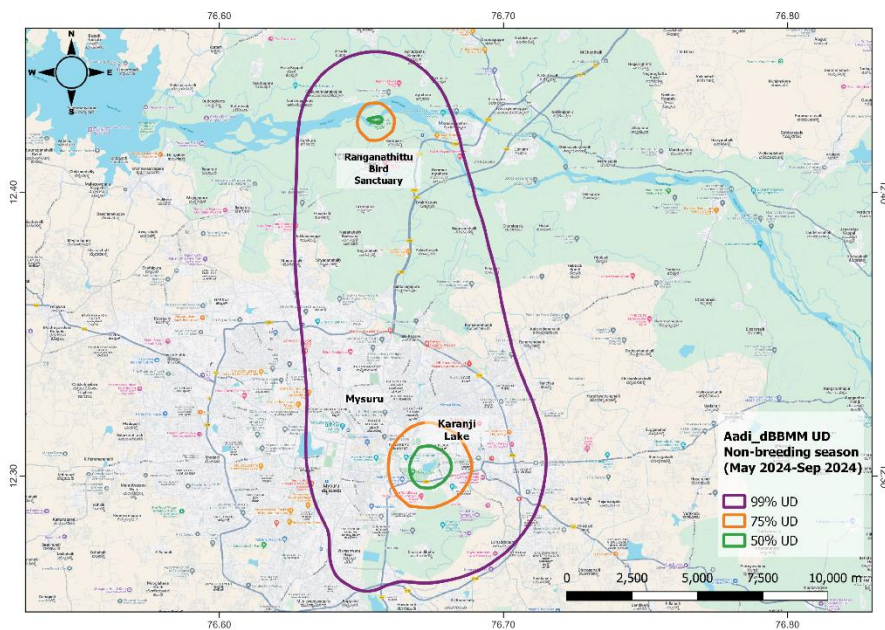
Adult pelican (Aadi) movement patterns

Aadi was tracked for 756 days, providing 108,864 GPS locations. Immediately after release, Aadi moved away from the release site, first travelling to lakes in Bengaluru (approximately 100 km from the release location), then to Mysuru (approximately 80 km from the release location). Throughout the tracking period, all movements remained within the Bengaluru–Mysuru geographical belt, demonstrating spatial fidelity to this corridor.

During the first non-breeding season (February to September 2023), Aadi's movements were broadly distributed across the Bengaluru–Mysuru belt. A few concentrated 50% core areas were evident (less than 1 sq. km), indicating spatially diffuse foraging patterns. The 75% UD encompassed 1 sq. km, centered on Kudlur Lake in a neighboring district, while the 99% UD extended to 907 sq. km, incorporating multiple urban lakes in both the Bengaluru and Mysuru regions. In the second non-breeding season (May to September 2024), ranging patterns contracted substantially. The 50% core area was recorded to be 2 sq. km, concentrated within a 10 km radius of Ranganathittu Bird Sanctuary in Mysuru and Karanji Lake. The 75% UD reduced to 1 sq. km (no change in absolute area but representing refined spatial concentration), and the 99% UD contracted to 152 sq. km, showing an 83% reduction compared to the first non-breeding season (Fig. 6.2).



(a)



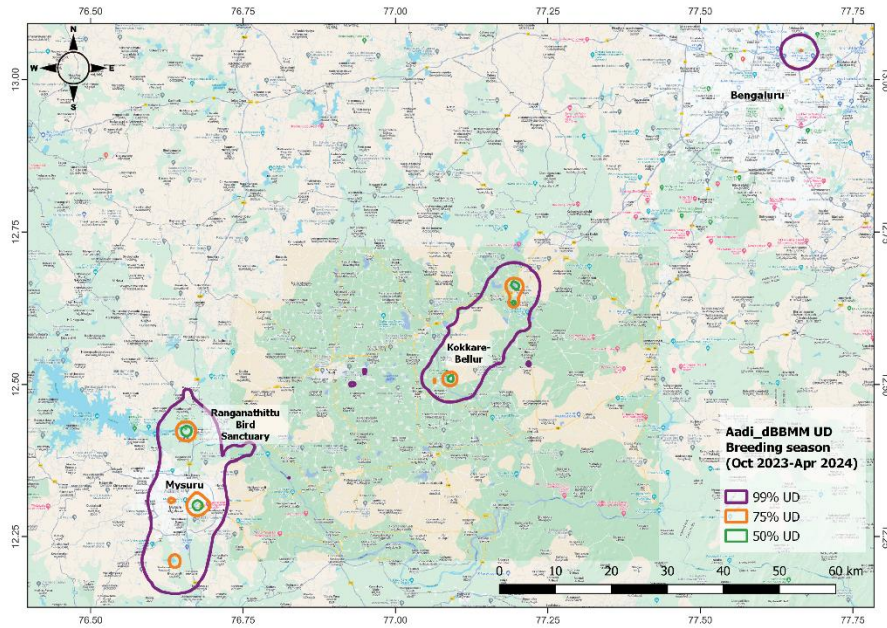
(b)

Figure 6.2. Non-breeding season utilization distributions (UD) of the adult Spot-billed Pelican (Aadi) derived from Dynamic Brownian Bridge Movement Models (dBBMM). The maps show a comparison between (a) the first non-breeding season (February–September 2023), characterized by wide-ranging movements across the Bengaluru–

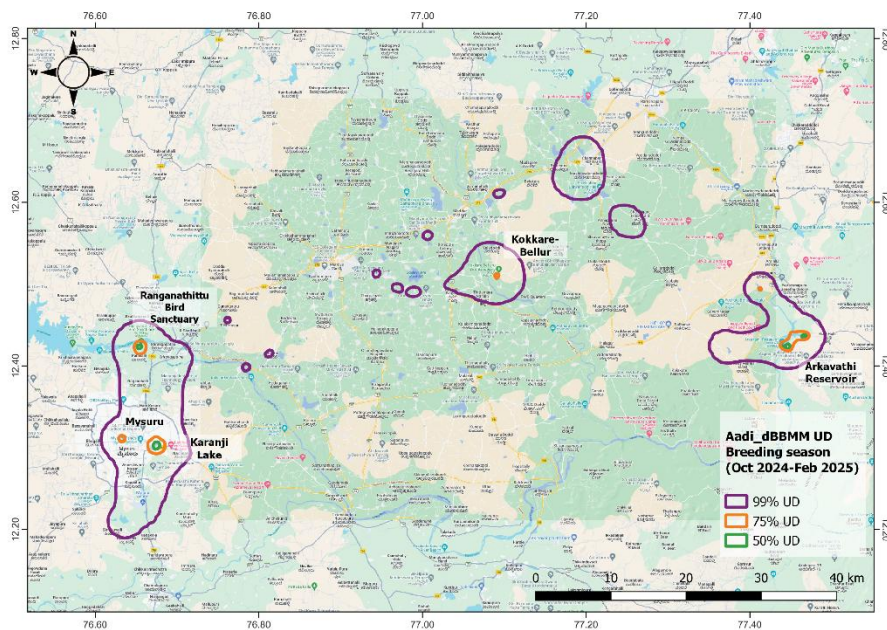
Mysuru corridor, and (b) the second non-breeding season (May–September 2024), showing a dramatic contraction and refinement of the core use areas around Mysuru.

Note that both maps are on independent scales.

During the first breeding season (October 2023 to April 2024), Aadi attempted breeding twice. The initial attempt at the release location (Kokkare Bellur) failed after one month of nesting. Following this failure, Aadi moved to Ranganathittu Bird Sanctuary and initiated a second nesting attempt, successfully producing one fledgling, as confirmed through photographic evidence by forest staff (personal communication). The 50% core area encompassed 8 sq. km, including both breeding sites and neighboring lakes, which represented foraging grounds. The 75% UD extended to 43 sq. km, whilst the 99% UD covered 703 sq. km, capturing movements between failed and successful breeding attempts and associated foraging areas. In the second breeding season (October 2024 to February 2025), Aadi bred only once at Ranganathittu. The 50% core area was reduced to 2 sq. km (a 75% reduction), encompassing Ranganathittu, a neighboring lake, and a distant reservoir located approximately 120 km from Ranganathittu. The 75% UD contracted to 12 sq. km (a 72% reduction), and the 99% UD decreased to 471 sq. km (a 33% reduction) (Fig. 6.3).



(a)



(b)

Figure 6.3. Inter-annual comparison of breeding season space use for the adult Spot-billed Pelican (Aadi). The dBMM utilization distributions (UDs) show (a) an extensive home range (99% UD: 703 km²) during the first breeding season (October 2023–April 2024), encompassing two nesting attempts. This is contrasted with (b) a more efficient,

contracted home range (99% UD: 471 km²) in the second breeding season (October 2024–February 2025), reflecting site fidelity to the successful Ranganathittu colony and the elimination of exploratory movements. Note that both maps are on independent scales.

Daily distance travelled (DDT) differed markedly between the adult (Aadi) and juvenile (Shimsha) and varied across seasons and years. For the adult pelican, Aadi, median daily distance travelled (DDT) increased consistently during breeding seasons relative to the preceding non-breeding periods. In 2023, the median DDT during the non-breeding season was 5.55 km (range: 1.96–99.2 km), increasing to 24.7 km (range: 1.56–151 km) during the 2023 breeding season. Similarly, in 2024, the median DDT increased from 1.39 km (range: 0.41–66.7 km) in the non-breeding period to 3.54 km (range: 0.39–73.3 km) during the breeding season. The juvenile pelican, Shimsha, showed consistent daily movement patterns across years, with comparatively narrower seasonal variation. During the first-year post-release (2022–2023), the median DDT was 8.8 km, with values ranging from 1.47 km to 68.7 km. In the second year (2023–2024), the median DDT increased to 10.9 km, while the overall range remained similar (0.41–67.6 km). Compared to the adult, Shimsha displayed higher median DDT values than Aadi during non-breeding periods, but lower maximum daily distances than those recorded by the adult during breeding (Fig. 6.4).

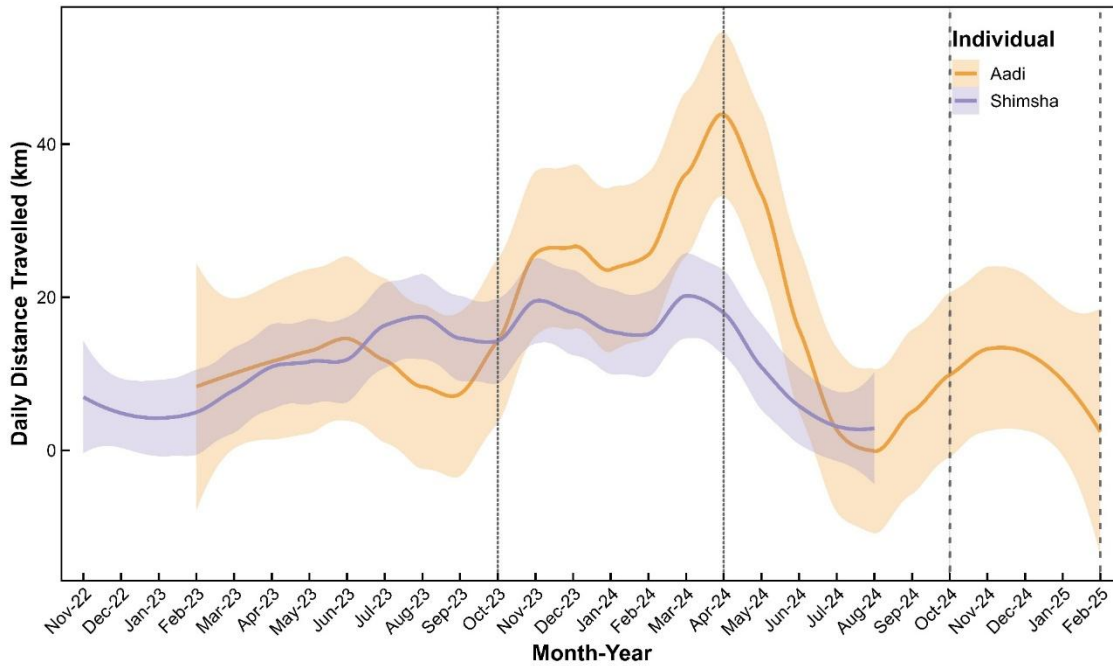


Figure 6.4. Comparison of age-dependent movement patterns in two Spot-billed Pelicans tracked using GPS telemetry. The juvenile (Shimsha) shows a progressive increase in daily distance travelled over time, whereas the adult (Aadi) exhibits a cyclical movement pattern with pronounced peaks in daily travel during breeding seasons, consistent with central-place foraging behavior. Vertical dashed lines indicate the onset and termination of Aadi’s breeding periods (October 2023–April 2024 and October 2024–February 2025). Lines represent LOESS-smoothed mean daily distance travelled, with shaded bands indicating 95% confidence intervals.

6. 4 Discussion

This case report provides novel insights into the post-release movement ecology of rescued Spot-billed Pelicans, revealing distinct ranging strategies between a hand-raised juvenile and a rehabilitated adult. The application of GPS telemetry, coupled with dBBMM analysis, enabled the precise quantification of utilization distributions and temporal dynamics in space use,

contributing to an understanding of individual-level variation in this Near Threatened species. The contrasting movement patterns between Shimsha and Aadi reflect fundamental differences in life-history stage and prior experience. Shimsha's gradual spatial expansion and increasing daily distances align with the ontogenetic development of foraging skills and spatial knowledge acquisition in juvenile waterbirds (Mendez *et al.* 2017). The progressive shift from localized movements near the release site to exploration of more distant wetlands suggests increasing independence and competence in identifying foraging opportunities.

In contrast, Aadi's immediate long-distance departure from the release site and rapid establishment of movements within the Bengaluru–Mysuru corridor indicate retention of spatial memory and navigational abilities despite rehabilitation. This behavioral pattern suggests that adult individuals possess prior knowledge of regional wetland networks, enabling them to navigate efficiently to known foraging and breeding areas (Baert *et al.* 2022). The restriction of movements to this corridor throughout the tracking period demonstrates spatial fidelity, a common trait among adult waterbirds with established home ranges.

Aadi's pronounced seasonal variation in space use, with contracted core areas during the second year, reflects habitat familiarity and optimized resource use. The dramatic reduction in non-breeding season UD size during Year 2, with movements restricted to the vicinity of Ranganathittu and Karanji Lake, suggests a refinement of foraging strategies and the identification of productive, reliable wetlands. Such spatial optimization has been documented in other colonial waterbirds, where experienced individuals concentrate their foraging effort in familiar, high-quality habitats rather than engaging in exploratory movements (Geary *et al.* 2020).

The breeding season patterns reveal reproductive site fidelity and flexible nesting strategies. The dual breeding attempts in Year 1, including a failed attempt followed by successful breeding at an alternative site, demonstrate behavioral plasticity in response to initial failure.

Site-switching following breeding failure is an adaptive strategy in colonial waterbirds, enabling relocation to sites with higher success probability (Danchin *et al.* 1998; Wilkinson and Jodice, 2022). The subsequent concentration of breeding activity at Ranganathittu in Year 2, accompanied by a reduced UD size, indicates the development of site fidelity following successful reproduction, a common pattern in long-lived colonial species (Boulinier and Danchin, 1997).

The elevated daily distances recorded for Aadi during breeding seasons reflect increased foraging effort associated with provisioning demands. Spot-billed Pelicans are known to travel substantial distances between breeding colonies and foraging wetlands (Kannan and Manakadan, 2005), and the observed 35 to 42 km/day movements during reproduction align with central-place foraging constraints. The post-breeding decline in daily distances suggests reduced energetic demands and potentially greater prey availability or accessibility during non-breeding periods.

Shimsha's progressive increase in daily distance reflects ontogenetic changes in foraging proficiency and energetic requirements. Hand-raised waterbirds often exhibit protracted development of optimal foraging behaviors compared to wild-reared conspecifics (Delord *et al.* 2024), and the gradual increase observed here suggests Shimsha acquired foraging skills over an extended period post-release. By Year 2, daily distances approached those of the adult during non-breeding periods, indicating functional integration into wild foraging patterns.

From a conservation perspective, the identification of Ranganathittu and associated lakes as critical year-round habitats for Aadi, as well as the Shimsha River corridor, highlights the importance of protecting wetland networks rather than isolated sites. Connectivity between breeding colonies and foraging wetlands is essential for pelican persistence, particularly given the seasonal variation in water availability across India's wetlands (Kannan and Pandiyan, 2013).

The successful post-release survival and breeding of Aadi over two consecutive seasons demonstrates the conservation value of rehabilitation and release programmes for Spot-billed Pelicans. The confirmed breeding success at Ranganathittu indicates that rehabilitated adults can successfully reintegrate into wild populations and contribute at the population level. Similarly, Shimsha's apparent successful transition to independent foraging suggests that hand-raised juveniles, despite extended human care, can develop necessary survival skills.

This case report is limited by a small sample size ($n = 2$), precluding statistical generalization to broader populations. Individual variation in movement ecology can be substantial, and the rescued status of these pelicans may influence ranging behavior compared to colony-reared individuals. Future studies should track larger samples, including wild-caught individuals across multiple colonies, to establish population-level movement patterns and identify whether rescued individuals exhibit behavioral differences. Additionally, this study focused on spatial patterns without integrating data on habitat characteristics or prey availability.

Future research should incorporate wetland productivity metrics, fish abundance data, and anthropogenic disturbance indices to model habitat selection and identify drivers of space use variation. The integration of accelerometer data could refine activity budgets and distinguish between foraging and non-foraging movements. Long-term tracking beyond two years would enable assessment of lifespan movement dynamics, breeding site fidelity over multiple seasons and potential dispersal patterns. For Shimsha, continued monitoring through sexual maturity would reveal whether juvenile spatial patterns predict adult home range establishment.

Chapter – 7

CONCLUSION: CONSERVATION AND MANAGEMENT OF WATERBIRDS IN KOKKARE-BELLUR

The culmination of this comprehensive five-year research on the population dynamics and nesting ecology of colonial waterbirds in the Kokkare-Bellur Community Reserve (KBCR), Southern India, has profound implications for the long-term conservation and site-specific management of resident and migratory waterbirds. By elucidating the interactions between climatic variables, interspecific nesting dynamics, habitat preferences, and foraging ecology, this study has translated theoretical ecological understanding into tangible, actionable conservation interventions at the grassroots level. The outcomes of this research have not only informed policy and conservation planning but have also significantly shaped the Karnataka Forest Department's strategic approach to managing the KBCR landscape.

Institutionalization of Nest Monitoring and Data-driven Management

One of the major outcomes of this study is the establishment of a standardized, long-term nest monitoring program for colonial waterbirds in KBCR. In collaboration with the Karnataka Forest Department, forest staff have been trained to carry out weekly surveys using pre-designed datasheets that record key parameters including nesting chronology, nest fate, tree preference, mortality events, and recruitment success. This initiative designed and initiated as part of the doctoral work has fostered a culture of data-backed conservation management.

Insights derived from **Objective 1** of this research on examining the role of rainfall in nesting initiation and success have helped in identifying temporal windows for active surveillance, tree pruning restrictions, and habitat enrichment, synchronized with nesting onset and peak

breeding periods. These adaptive practices ensure minimal disturbance during vulnerable phases of chick rearing and maximize nest survival across species.

Habitat Restoration and Plantation Strategy

Research findings from **Objective 2**, which explored niche partitioning and tree preference among sympatric colonial nesters, have guided tree enrichment and habitat restoration across the village landscape. Species-specific tree preference was documented, showing strong affinities of Spot-billed Pelicans for Tamarind (*Tamarindus indica*) and Banyan (*Ficus benghalensis*), Painted Storks for Portia (*Thespesia populnea*) and White Gulmohar (*Delonix elata*), and smaller waterbirds for interior canopy areas of mixed-species trees.

Informed by this data, plantation efforts were undertaken inside and along the periphery of the village, with over 250 native and preferred tree saplings planted between 2020 and 2023. New tree patches have been strategically created near critical areas like schools and waterbodies to facilitate future nesting. Regular watering, patrolling, and soil enrichment around existing mature trees have helped enhance tree health and reduce the likelihood of storm-induced uprooting a major threat identified in this study.

Infrastructure for Rescue, Rehabilitation, and Veterinary Support

Addressing the conservation threats identified under **Objective 3**, particularly chick mortality from nest falls and adverse weather, led to the development of dedicated avian rescue infrastructure in the village. A fully functional rescue facility was established with provisions for first-aid, hand-raising, and fledgling care. This facility is managed by trained local personnel and forest watchers and is equipped to support 50–60 birds simultaneously during peak breeding season.

Further, based on this study's findings and the observed need for structured post-rescue acclimatization, a proposal was submitted to the Karnataka Forest Department to construct a shallow pond adjacent to the rescue facility. This pond is envisioned to serve as a controlled space for soft release and the development of self-feeding behaviors in hand-raised, semi-aquatic chicks, particularly Spot-billed Pelicans and Painted Storks. By mimicking natural foraging conditions, such an environment would enhance survival outcomes during the critical transition from captivity to the wild. The Forest Department has taken this recommendation under consideration as part of its future conservation infrastructure planning for Kokkare-Bellur.

Over 200 birds have been rescued and reared between 2020 and 2022, with a documented survival rate exceeding 85%, marking a significant milestone in ex-situ conservation within a community reserve setting. Weekly morphometric monitoring and chick growth charts developed as part of this doctoral research have been adopted as a protocol by the Forest Department for tracking chick health and developmental anomalies. The application of such standardized rehabilitation practices is expected to be replicable across other community-based bird conservation sites in India.

Foraging Ecology and Landscape Management

Building upon **Objective 4**, which mapped the seasonal foraging habitats and ranging dynamics of the Spot-billed Pelican, management strategies now incorporate a landscape-scale perspective. Eighteen key waterbodies were identified as critical foraging sites through direct observations and tracking studies. These wetlands have been regularly monitored for water quality, fish availability, and encroachment pressure.

Regular anti-viral spraying under nesting trees, initiated as a preventive step in response to previously observed mass mortality events, is now a routine seasonal activity. Water samples

from known foraging lakes are being collected annually and analyzed to identify pollutant loads and mitigate contamination from agricultural runoff and industrial effluents.

These measures, collectively informed by ecological data, help ensure year-round habitat continuity, especially during non-breeding periods, when birds shift their ranging patterns towards larger water bodies.

Community Engagement and Conservation Incentives

Recognizing the indispensable role of community participation in KBCR's protection, this research led to the revitalization of village-based engagement programs. Drawing from the socio-ecological values of coexistence, a compensation scheme was formalized for 71 villagers who own trees used for nesting. Each tree was geo-tagged, inventoried, and categorized based on species, utility, and nesting frequency. Compensation values were aligned accordingly, encouraging tree retention.

To foster positive behavioral shifts, homes receiving compensation were also provided with solar lighting units and access to subsidized drinking water through a new purification unit installed in the forest quarters. This integrated benefit-sharing model serves both conservation and development goals.

Educational materials such as brochures, books, interpretation boards were created and distributed to schools and tourist centers. Skits, street plays, and drawing competitions organized in collaboration with drama societies and NGOs have enhanced awareness across age groups. These initiatives, initially conceptualized and implemented as outreach components of the PhD project, have now become integral to annual Forest Department programs.

Policy Contributions and Scientific Legacy

The findings and methodologies developed through this dissertation have shaped local and regional conservation policy. For the first time, ecological principles such as niche partitioning, vertical stratification, and temporal breeding overlap were applied to micro-scale habitat management in a community reserve. This site-level integration of academic research with administrative action offers a replicable model for decentralized conservation planning.

Furthermore, this research contributed to the Forest Department's decision to fund long-term ecological monitoring in KBCR. As a result, additional tagging of birds and trees, digitized population trend mapping, and collaborative studies with veterinary universities are now in motion.

Recommendations and Future Directions

While significant strides have been made, continued success depends on sustained ecological research, community sensitization, and institutional commitment. The following recommendations are proposed:

1. **Institutionalize Research Presence:** A permanent research station or field lab should be established in Kokkare-Bellur to facilitate long-term ecological and veterinary studies.
2. **Expand Tagging and Tracking Efforts:** Scale-up patagial tagging and GPS tracking across more individuals and species to better understand landscape connectivity and habitat use.
3. **Wetland Restoration and Water Management:** De-siltation and habitat restoration of foraging wetlands should be prioritized, with seasonal fish stock assessments and pollution controls implemented in collaboration with local panchayats.

4. Climate Adaptive Management: Develop early-warning systems for extreme weather events that can damage nests. Community-level disaster preparedness can reduce mortality from storms.
5. Revival of Hejjarle Balaga: The once-active village conservation group should be formally integrated as a Forest Department partner for youth-led awareness campaigns and community patrolling.
6. Digital Tools and Citizen Science: A mobile-based app could be developed to crowdsource nesting and sighting data from birdwatchers and villagers, aiding in real-time monitoring and wider public engagement.
7. Replication at Other Sites: The KBCR model should be documented as a case study for replication in other community reserves and Important Bird Areas (IBAs) with similar ecological and socio-cultural settings.

The study of colonial waterbird ecology at Kokkare-Bellur has underscored the value of interdisciplinary, field-based research in informing place-based conservation strategies. Through detailed ecological analyses, habitat mapping, and proactive engagement with local stakeholders and forest managers, this work has bridged the gap between science and action. Kokkare-Bellur stands today not only as a unique heronry but also as a beacon of community-driven conservation success—one that illustrates the power of coexistence, evidence-based management, and enduring stewardship of our avian heritage.

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ANNEXURE-1

(a) Mahapatra, A. (2026). Spotting the difference: Sexual size dimorphism and individual identification in the Spot-billed Pelican *Pelecanus philippensis*. Journal of Wildlife Science (Accepted) [ISSN (online): 3048-7803].

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Ref.: Ms. No. JWLS-26-0015R1
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Journal of Wildlife Science

Dear Ms. Mahapatra,

I am delighted to inform you that your manuscript has been accepted for publication in Journal of Wildlife Science, following the recommendations from academic editor and the reviewers.

It was first submitted on 19 Jan 2026 and accepted on 27 Jan 2026 after a thorough peer review process.

The production team will contact you shortly to address any final queries and coordinate the publication process.

Thank you for choosing Journal of Wildlife Science as the platform for sharing your research. We appreciate your contribution and look forward to featuring your work.

With kind regards

MEWA SINGH, Ph.D.
Editor-in-Chief
Journal of Wildlife Science

Editor's comments:

Reviewers' comments:

Spotting the difference: Sexual size dimorphism and individual identification in the Spot-billed Pelican *Pelecanus philippensis*

Abstract

In the Spot-billed Pelican (*Pelecanus philippensis*), sexes are phenotypically monomorphic, though a slight size difference is suspected. This study aimed to determine the extent of sexual size dimorphism (SSD) by examining ten morphometric characters from 41 adult pelicans (18 males, 23 females) found dead at Kokkare-Bellur Community Reserve, India, between 2018 and 2022. The pelicans were surgically sexed for confirmation. Males were found to be significantly larger than females in nine of the ten measurements. Notably, culmen length showed a clear distinction with no overlap; lengths less than 320 mm were classified as female and more than 337 mm as male. Comparison of wild pairs through digital photographs confirmed this dimorphism. Furthermore, unique spot patterns on the beak of each individual were discovered, which can facilitate non-invasive individual identification for future behavioral investigations.

Key words: beak spots, culmen length, digital photographs, morphometrics, sexual size dimorphism, Spot-billed Pelican

Introduction

In the avian world, over 50% of species are considered monomorphic, with sexes being indistinguishable in plumage (Griffiths *et al.*, 1998). However, sexual size dimorphism (SSD) often exists where reproductive roles are segregated, frequently associated with sex-specific behaviors and life-history strategies (Liker *et al.*, 2021; Fairbairn *et al.*, 2007). While males are often the larger in birds, notable exceptions exist such as Falconiformes, Strigiformes, Charadriiformes (Fairbairn, 1997). The larger female may be advantageous for incubating larger clutches, defending nests or competing with partners like in Jacanas (Emlen and Wrege,

2004). In the family Pelecanidae, although sexes generally appear alike, male-biased SSD is known to occur; for instance, it has been determined in the American White Pelican (*Pelecanus erythrorhynchos*) (Dorr *et al.*, 2005). In the case of Spot-billed Pelican *P. philippensis* sexes are again reported to be alike (Ali and Ripley, 1978), though males may be larger.

The Spot-billed Pelican is among the smallest of the old-world pelicans and is a tree-nesting species. Its historical range across South Asia has contracted significantly, and it is now confined to smaller pockets in India, Sri Lanka, Thailand, Cambodia, and Sumatra (BirdLife International, 2017). Due to a declining population, the species is classified as Near Threatened (BirdLife International, 2017). Southern India hosts 21 known breeding colonies, primarily in coastal regions (Subramanya, 2006), though additional unreported breeding sites may exist. An exception is the inland pelicanry at Kokkare-Bellur in Karnataka, believed to be one of the oldest nesting sites in southern India, where pelicans have nested within the village for over 300 years (Manu and Jolly, 2000; Neginhal, 1977).

In 2017-18, this site witnessed a large-scale mortality of adult pelicans, which was potentially linked to gastrointestinal parasitic infections (Kumar *et al.*, 2019). This alarming event prompted the Karnataka State Forest Department to initiate a long-term monitoring project in 2018. Following this, over the course of four breeding seasons (2018-22), the pelicans that died were first measured for their morphometry and then sexes were identified through the surgical post-mortem. This note utilizes these specimens to provide the first detailed quantification of SSD in the Spot-billed Pelican using morphometric data. It further explores the reliability of using these findings, particularly culmen length, and digital photography to sex pelicans in the wild, thereby providing a valuable, non-invasive tool for conservation research on this Near Threatened species.

Morphological information was recorded from these dead pelicans, including: Head length, culmen length, culmen width between nares, culmen width maximum, culmen depth, tarsus

length, tarsus width, mid-toe length, measured to the nearest 0.02 mm using Vernier Caliper (Aerospace 300 mm). Tail and wing chord length were measured to the nearest 1 mm using a ruler. The details of the measurements are provided in Fig. 1. All specimens were confirmed to be breeding adults through surgical examination of the reproductive organs during post-mortem. Body mass was intentionally excluded from the analysis as the specimens were in poor physiological condition due to parasitic infections, which would have significantly skewed this variable. However, the skeletal and keratinized structures measured are inherently stable and not subject to the rapid atrophy seen in soft tissues. To assess field applicability, culmen lengths were compared using calibrated ratios derived from digital photographs of known breeding pairs. Digital photographs of wild pelican pairs were obtained using Canon PowerShot SX60HS (zoom range: 3.8-247mm) after a pair's gender was determined following a mating event. The male mounts over the female and holds her neck for a brief period of time while they mate. This was an essential step since the Spot-billed Pelican builds its nests in clusters, which means that multiple nests will be joined to form a single platform, making it difficult to tell which sexes and pairings they belong to. To minimize measurement errors, we implemented the following controls: Only photographs where both individuals' beaks were in the same plane and at similar angles relative to the camera were selected; Only photographs showing both pair members in lateral profile with beaks parallel to the camera plane were used. A total of 36 photographs (from an initial pool of >80 images) met these stringent selection criteria for image processing in Adobe Photoshop CS6 to draw lines and measure line length in pixels. Sex-wise differences were evaluated using non-parametric statistics, and sexual size dimorphism was quantified using a mean difference index ($MDI = (\text{mean female}/\text{mean male}) \times 100$) as proposed by Delestrade (2001) to determine the degree of dimorphism in each morphological character.

Result

The comparison of morphological characters in 18 male and 23 female Spot-billed Pelicans showed significant differences in nine of the ten characters measured. SSD ranged from 4-14% between sexes, with the mean difference index (MDI) exceeding 80% for all characters. Males were substantially larger than females, particularly in head and culmen length (14% larger) and tarsus width and length (10-13% larger) (Table 1).

Although the means for nine measurements were larger for males, there was overlap in the range of values for all characters except for culmen length. This measurement proved to be a definitive diagnostic tool, the culmen of males was consistently longer than 337 mm, while the culmen of females was always less than 320 mm (Fig. 3).

The reliability of using culmen length to sex pelicans in the wild was tested by analyzing 36 digital photographs of known pairs (Fig. 2). The ratio of male to female culmen length, calculated from these images, confirmed that males possess a longer beak, with an average ratio of 1.19 ± 0.09 .

To enhance field identification methods, other physical attributes were compared. This investigation revealed no reliable differences between sexes in the presence of a crest, plumage coloration, or eye-patch color. Both sexes displayed a crest, over 90% of individuals had white plumage, and the majority of both males and females exhibited pale yellow eye-patches. However, the study revealed that the spot patterns on the beak were unique to each individual. These patterns, varying from triangular and alphabet-shaped spots to continuous lines formed by converging spots, serve as a natural marker (Fig. 4). This provides a method for identifying individual birds for further scientific investigation.

Discussion

In the family Pelecanidae, which contains 8 species in the genus *Pelecanus* worldwide, information on SSD is scanty. Most of the available information on morphometry is based on a handful of museum specimens, which suggests that males are larger than females (Marchant

and Higgins, 1990; Ali and Ripley, 1978). Our results clearly show that in Spot-billed Pelicans, males are larger. Male-biased SSD is a common attribute seen in waterfowl (Székely *et al.*, 2007). The advantages of males being larger have been explained with respect to contests over mates or resources, mate preferences by the opposite sex, and resilience to temporary food shortages (Székely *et al.*, 2007). However, the reasons for the male-biased SSD in Spot-billed Pelicans are still unclear, as there is no information available on the sex differences in breeding behavior and ecology.

Significant SSD was found in nine of the ten morphological characters considered in this study. However, culmen length alone showed clear distinction with no overlap, which can be used to determine the sex of adult Spot-billed Pelicans. A similar lack of overlap in culmen length was utilized to successfully determine the sex of the American White Pelican (*P. erythrorhynchos*) (Dorr *et al.*, 2005). While our results provide a clear threshold for the Kokkare Bellur population, it remains to be seen if this "zero overlap" holds across other geographically separated populations or if these specific values are population-specific. Currently, no other studies have been conducted in India or other regions within the species' range to provide a comparative baseline. Simple linear measurement of the beak has been used to predict sex in many other waterbirds (e.g., Riordan and Johnston, 2013; Devlin *et al.*, 2004; Murata *et al.*, 1988). The size of the culmen may be affected by both inter- and intrasexual selection (De Marchi *et al.*, 2012). The longer beak may allow males to produce loud clapping sounds to attract females, or to threaten potential predators. While bill-clapping is a recognized display in the genus *Pelecanus*, the specific relationship between culmen dimensions and acoustic properties in Spot-billed Pelicans warrants further bioacoustic investigation. During mating, when the male mounts the female, males with longer beaks may be at an advantage when they use their beaks to grasp the females' necks (Gokula, 2011). Longer beaks in males may also be a result of greater fitness through sexual selection, as they allow males to more efficiently

harvest food resources (Bildstein, 1987) or gather nesting material (Urfi and Kalam, 2006). The culmen is also likely to be more useful for identifying the sex of pelican carcasses, as it degrades more slowly than softer tissues (Dorr *et al.*, 2005).

Sexing birds using digital photographs has been tested before and proved to be highly reliable, non-invasive method to sex individuals (Williams *et al.*, 2020; Weckauf and Handschuh, 2011; Urfi and Kalam, 2006; Cheong *et al.* 2007). Such non-invasive techniques are particularly valuable for morphometric studies on wild, free-ranging animals on the Indian subcontinent, where capturing may not be feasible (Mahendiran *et al.*, 2018). This method has also helped as a tool to understand social interactions of species, such as larger Painted stork (*Mycteria leucocephala*) males which acquired better nesting sites over territorial winning from smaller conspecifics (Urfi and Kalam, 2006). Males of White Ibis (*Eudocimus albus*) during nesting were found to be more agile in stealing prey than females as they were more efficient in intimidating others (Frederick, 1985). Foraging efficiency when compared between male and female Oriental White Storks (*Ciconia boyciana*) revealed sex-based differences in foraging habitats and methods of foraging (Sung *et al.*, 2009).

Likewise, this study can be useful in easy identification of sex in field for studying sex-specific social, nesting and foraging behavior, understanding energetics, parental investments, effects of differential sex ratio in population. Future research should specifically leverage these sexing techniques to explore the ecological impacts on mortality across varying habitats. In particular, at sites like Kokkare Bellur, comparing the survival rates of Spot-billed Pelicans in man-made wetlands versus their natural habitats could reveal if sex-specific vulnerabilities exist. Understanding these mortality drivers is critical for the long-term conservation of the species. Once a mating pair has been identified in field, the male and female can be distinguished by the differences in their beak length. As the pairs are rarely observed together during the breeding season apart from the mating and nest building events, researchers should virtually

mark the individuals based on their unique beak spots. This method will aid in conducting detailed scientific investigations on their nesting behavior.

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Table 1. Comparison between male and female adult breeding Spot-billed Pelicans. Descriptive statistics are given as mean (\pm standard deviation) and minimum-maximum values. *P* values are significant <0.05 except *marked where it was not significant for Mann-Whitney U test.

Measurement	Male	Female	<i>Mann-Whitney U</i> statistic	MDI (%)
	<i>n</i> = 18 Mean \pm SD (range)	<i>n</i> = 23 Mean \pm SD (range)		
Head length (mm)	442.6 \pm 20.6 (412-480)	383.4 \pm 18.2 (345-420)	1.50	86.6
Culmen length (mm)	350.8 \pm 11.7 (337-377)	303.3 \pm 8.4 (287-320)	0.00	86.4
Culmen width between nares (mm)* <i>P</i> value = 0.474	20.6 \pm 2.0 (18-25)	21.6 \pm 4.3 (12-30)	234.00	95.3 [#]
Culmen width max. (mm)	37.7 \pm 1.8 (35-41)	33.6 \pm 3.4 (25-40)	62.00	89.1
Culmen depth (mm)	34.6 \pm 4.5 (25-41)	31.7 \pm 2.8 (26-36)	125.00	91.6
Tarsus length (mm)	95.6 \pm 10.0 (76-112)	84.1 \pm 11.8 (60-100)	102.50	87.9

Tarsus width (mm)	24.3 ± 1.9 (22-27)	21.8 ± 2.2 (19-26)	86.00	89.7
Mid-toe length (mm)	121.4 ± 10.6 (100-142)	111.2 ± 7.0 (100-125)	92.50	91.5
Tail length (mm)	212.7 ± 36.0 (160-280)	185.5 ± 29.6 (120-246)	118.00	87.2
Wing chord length (mm)	533.4 ± 28.0 (504-596)	513.8 ± 8.5 (500-530)	117.00	96.3

Mean difference index (MDI) calculated as (mean female/mean male) × 100. # = MDI = mean male/mean female × 100.

Figure 1. Linear morphological measurements taken of adult Spot-billed Pelicans.

Figure 2. A nesting pair of Spot-billed Pelican at Kokkare-Bellur Community Reserve, southern India. The male is larger with a long beak right of the female during a courting incident. L1 (female) and L2 (male) depicts culmen length considered during measurement in Adobe Photoshop CS6.

Figure 3. Box plots showing the variation in morphological characters in male and female Spot-billed Pelicans. The thick horizontal stroke inside the box shows the median, the box represents the interquartile range, the vertical line extending from box represents standard deviation and the shaded circles show the data points. All the graphs show significant differences (P value > 0.05 except in the case of Culmen width between nares which doesn't have significant difference P value = 0.474).

Figure 4. Variation in beak spot patterns of Spot-billed Pelican pairs photographed during breeding time at Kokkare-Bellur. A-I are the nine pairs and the black circles in the beak depict their unique spots.

Figure 1.

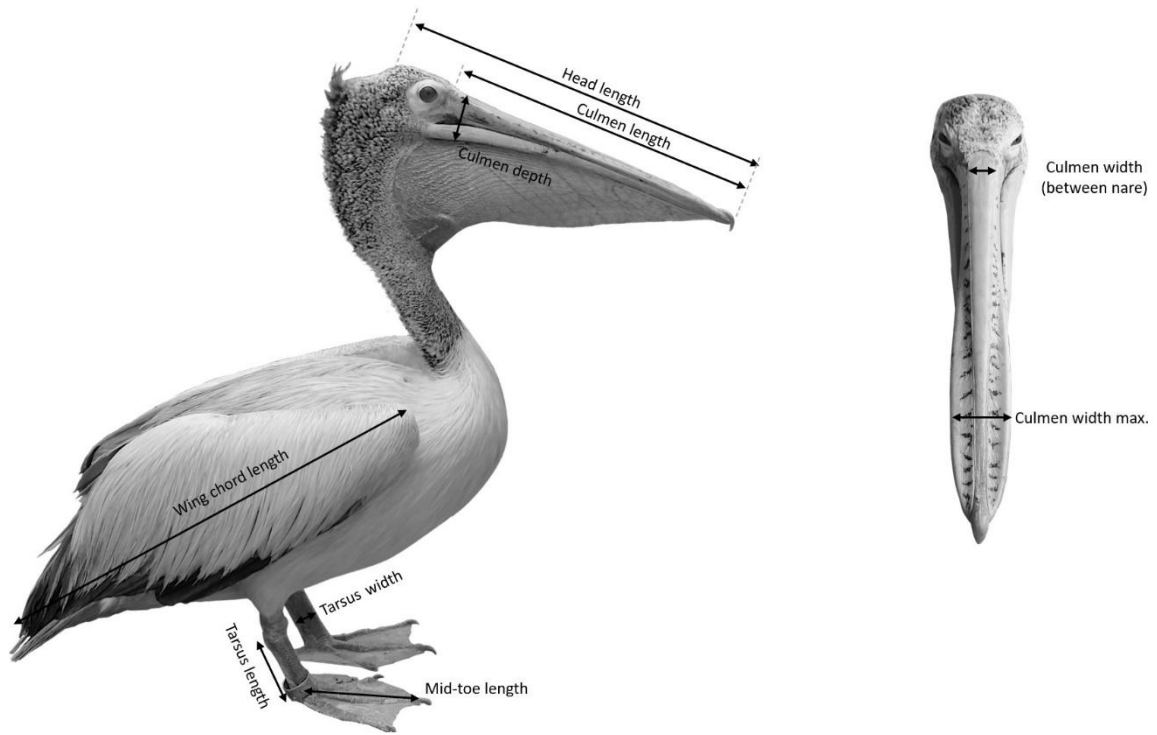


Figure 2.



Figure 3.

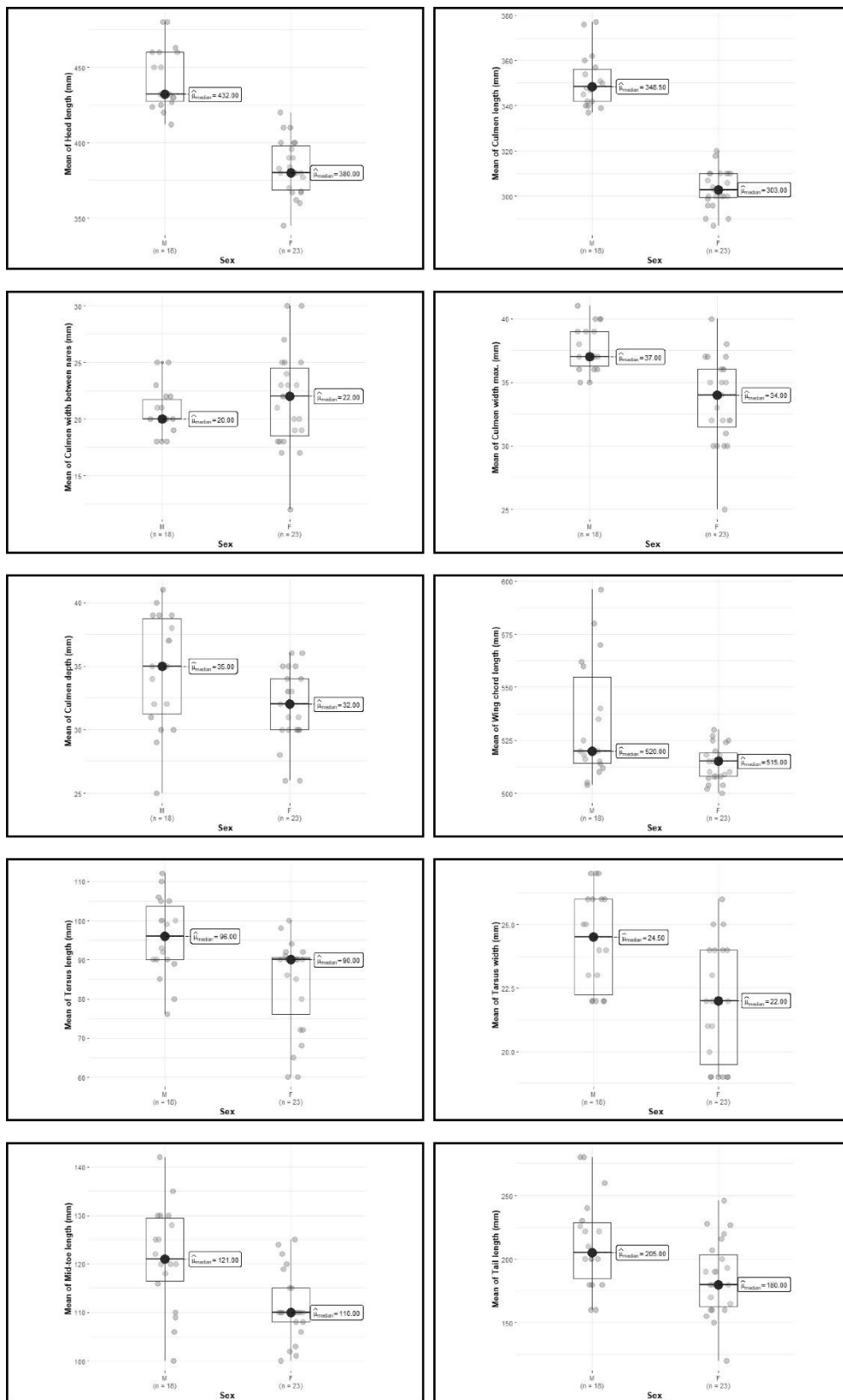
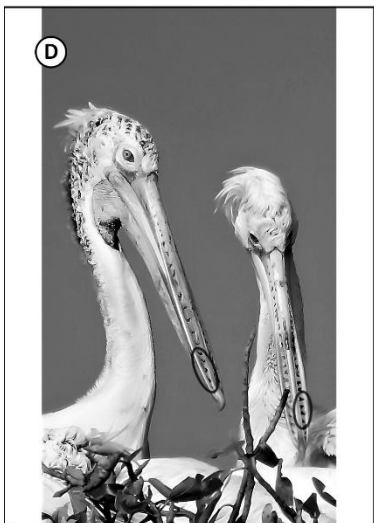


Figure 4.



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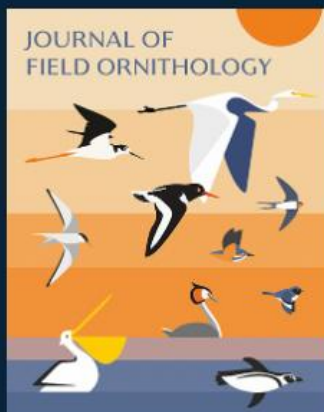
Nest partitioning in a mixed-species waterbird colony in a human-dominated landscape of Southern India

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Section:	Avian Behavior, Ecology, and Evolution	
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ANNEXURE-2



Aug. 24, 2025

To Whom It May Concern

This letter confirms that Aksheeta Mahapatra, Ph.D. Scholar, Wildlife Institute of India, attended the Waterbird Society 45th Annual Meeting that took place virtually on November 9-12, 2021, and made an oral presentation of her work titled "Birds of different feather also flock together: Spatial and temporal nesting patterns in a mixed species heronry in southern India".

Thank you,

Nellie Tsipoura
President Elect, Waterbird Society

(International Conference: Waterbird Society 2021)



Aug. 24, 2025

To Whom It May Concern

This letter confirms that Aksheeta Mahapatra, Ph.D. Scholar, Wildlife Institute of India, was an invited speaker at the “Pelicans of the World Symposium” that took place at the Waterbird Society’s 43rd Annual Meeting, Maryland, USA, November 6–9, 2019. She presented her work “Changing times and changing attitudes: Spot-billed Pelican *Pelecanus philippensis* conservation at the Kokkare-Bellur Community Reserve”.

Thank you,

Nellie Tsipoura
President Elect, Waterbird Society

(International Conference: Waterbird Society 2019)

**NATIONAL
SYMPOSIUM ON
AVIAN BIOLOGY**

IN CONJUNCTION WITH

2ND MEETING OF **ASSOCIATION OF
AVIAN BIOLOGISTS
IN INDIA**

CERTIFICATE

This certifies that

Aksheta Mahapatra

has participated and presented a talk in the

NATIONAL SYMPOSIUM ON AVIAN BIOLOGY

which was held at

IISER TIRUPATI, INDIA

between

07 to 10 DECEMBER 2019.



DINESH BHATT
PRESIDENT, AABI



V. V. ROBIN
CONVENER, IISER TIRUPATI



(National Conference: National Symposium of Avian Biology 2019)